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KENYAPITHECUS POSTCRANIAL SPECIMENS FROM NACHOLA, KENYA

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ABSTRACT Twenty nine postcranial specimens of a *Kenyapithecus* species, discovered at Nachola during the field seasons 1984 and 1986, are described in detail. The specimens come from baboon-sized animals, with a baboon-like degree of sexual dimorphism in size. This species of *Kenyapithecus* was a predominantly arboreal animal, utilizing a combination of pronograde quadrupedalism and orthograde climbing and clambering activities. Postcranially it most resembles *Proconsul*, but it is a slightly more derived hominoid.

Key Words: Hominoid, Kenya, *Kenyapithecus*, Miocene, Nachola, postcranials.

INTRODUCTION

The specimens described here were all collected in the years 1984 and 1986 by a joint Japan-Kenya Expedition directed by H. Ishida. The specimens come from the Nachola area of northern Kenya. Numerous specimens of the medium-sized *Kenyapithecus* have been recovered from Nachola, together with specimens of a small hominoid (Kunimatsu, 1992a, 1992b). These specimens have been recovered from localities that have been variably dated at 11-12 Ma (Matsuda *et al.*, 1984, 1986), 13-15 Ma (Itaya and Sawada, 1986), and 16-17 Ma (Pickford *et al.*, 1986). The twenty nine *Kenyapithecus* postcranial specimens are listed in Table 1, and described below.

DESCRIPTIONS OF THE FOSSIL SPECIMENS

Proximal right ulnae KNM-BG 15071 and 17824 (Fig. 1)

Introduction: KNM-BG 15071 is a 2.3 cm long proximal right ulnar fragment that preserves the most distal part of the trochlear notch and the most proximal part of the shaft. The trochlear notch surface is heavily eroded, as are the proximal and distal ends of the specimen. For the average of four measurements the specimen is

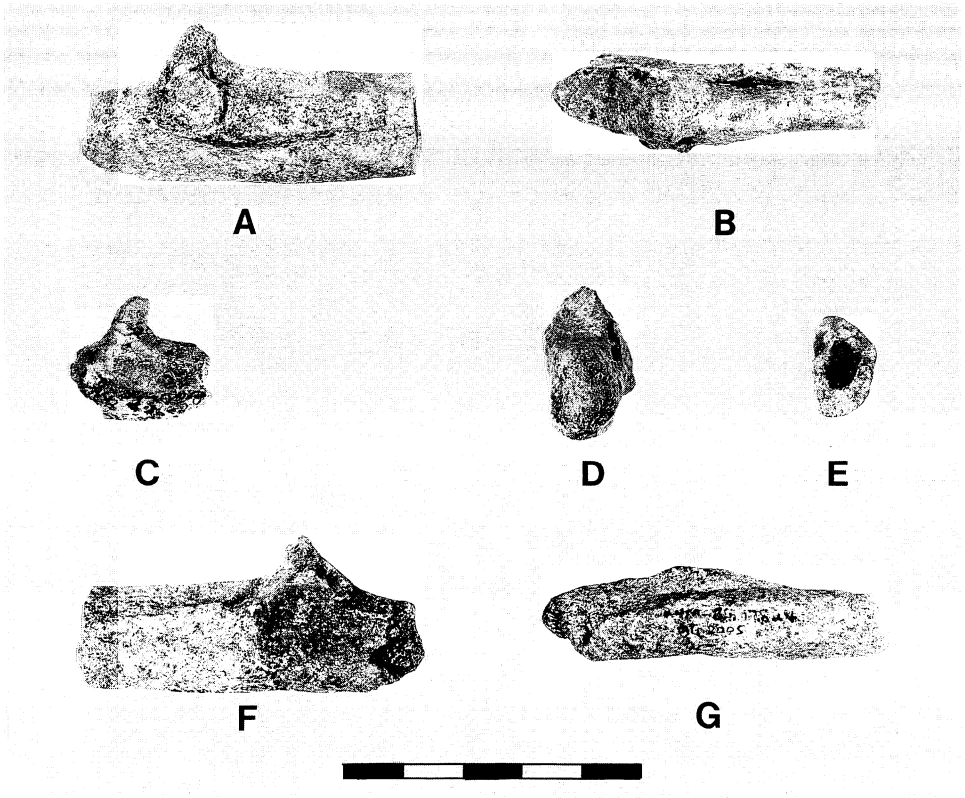

Figure 1. KNM-BG 17824 right ulna. A, lateral; B, anterior; D, proximal; F, medial; G, posterior views. E is the distal cross section. Anterior is towards the top of the page in D and E. C is a lateral view of KNM-BG 15071 right ulna for size comparison with KNM-BG 17824. Scale in cm.

Table 1. Specimen list.

Accession number	Bone	Site
KNM-BG 17826	Thoracic vertebra	BGI
KNM-BG 15527	Lumbar vertebra	BGI
KNM-BG 17822	Sacral vertebra	BGI
KNM-BG 15071	Right ulna	BGO
KNM-BG 17824	Right ulna	BGI
KNM-BG 15541	Metacarpal	BGI
KNM-BG 17807	Metacarpal	BGI
KNM-BG 15533	Femur	BGX
KNM-BG 15536	Femur	BGX
KNM-BG 17775	Femur	BGX
KNM-BG 17816	Right femur	BGI
KNM-BG 17819	Right femur	BGI
KNM-BG 17820	Left femur	BGI
KNM-BG 17821	Femur	BGI
KNM-BG 15535	Left patella	BGR
KNM-BG 17809	Right fibula	BGI
KNM-BG 17810	Right fibula	BGI
KNM-BG 15529	Right talus	BGX
KNM-BG 17805	Right calcaneus	BGI
KNM-BG 17814	Right first metatarsal	BGI
KNM-BG 15531	Proximal phalanx	BGX
KNM-BG 17774	Proximal phalanx	BGX
KNM-BG 17811	Right proximal phalanx	BGX
KNM-BG 17813	Hallucial proximal phalanx	BGI
KNM-BG 15540	Middle phalanx	BGI
KNM-BG 17808	Middle phalanx	BGI
KNM-BG 17812	Middle phalanx	BGX
KNM-BG 17818	Terminal phalanx	BGI
KNM-BG 17748	Terminal phalanx	BGX

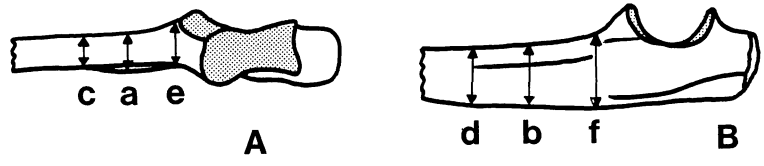

Figure 2. *Colobus polykomos* right ulna in anterior (A) and medial (B) views, showing measurements taken (see also Table 2).

Table 2. Ulnar indices and size comparisons.

	Index 1 Shaft proportions a×100/b[1]	Index 2 Shaft proportions c×100/d	Size a+b+e+f/4
Pan troglodytes[2]	77.2[3]	79.0	19.7
	67-94	67-94	17.6-21.9
	9.0	8.6	
Hylobates spp.	79.1	71.3	8.6
	60-97	60-82	7.7-9.4
	12.8	8.2	
Papio cynocephalus	—	—	12.2
Female			11.0-13.7
Papio cynocephalus	—	—	15.6
Male			14.6-16.9
Cercopithecus mitis	56.7	59.6	8.0
	47-65	51-63	5.9-9.9
	6.3	3.7	
Colobus polykomos	58.4	54.35	10.5
	47-65	45-66	8.1-11.3
	4.9	6.3	
Ateles spp.	65.0	62.8	8.8
	55-73	52-71	7.7-10.6
	5.9	6.6	
Cebus spp.	54.6	54.2	7.6
	47-65	46-66	6.0-8.9
	5.8	6.1	
Kenyapithecus sp.			
KNM-BG 17824	71.9	59.8	16.6
KNM-BG 15071	76.7	—	11.7
Aegyptopithecus zeuxis			
DPC 23940	58.0	62.5	9.9
Pliopithecus vindobonensis			
Individual 2	54.6	59.6	9.7
?*Dendropithecus macinnesi*			
KNM-SO 5537	55.6	54.0	8.9
Proconsul heseloni			
KNM-RU 2036CF	79.0	—	11.7
Proconsul nyanzae			
KNM-RU 1786	70.1	—	20.8
Proconsul major			
KNM-SO 5529	—	70.0	—
Dryopithecus brancoi			
RUD 22	71.3	—	13.4

[1] These are the measurements illustrated in Figure 2.

[2] $n=10$ for combined sex samples, $n=5$ for male and female samples.

[3] Mean, range and S.D.

similar in size to small female *Papio* ulnae (Table 2, Size and Fig. 2). KNM-BG 17824 is a 5.8 cm long proximal right ulnar fragment that preserves part of the trochlear notch and the proximal part of the shaft. The distal half of the trochlear notch is present, but is heavily eroded around all its margins, including the region of junction with the radial notch. The specimen is similar in size to large male *Papio* ulnae (Table 2, Size). KNM-BG 15071 is approximately 70% as large as KNM-BG 17824. The size ratios between the smallest female and largest male in the comparative samples (*Hylobates* excepted) range between 65% and 74%, while average values range between 78% and 93%. If KNM-BG 15071 is in fact from an adult female individual, rather than a juvenile, this ratio implies a degree of sexual size dimorphism in *Kenyapithecus* that is within the range seen in extant anthropoid samples, but perhaps slightly greater than is usual.

Description: The following is based on the morphology of the more complete specimen, KNM-BG 17824, except for features of the distolateral part of the trochlear surface and the adjoining radial notch, which are better preserved on KNM-BG 15071. The trochlea notch is bounded distally by an upright coronoid process that extends anteriorly beyond the radial notch, as found in extant large hominoids (Fig. 3, a). In addition, the radial notch faces almost directly laterally, as in extant hominoids (Fig. 3, b). However, the preserved lateral part of the distal margin of the trochlear notch is transversely aligned, as in most platyrrhines (Fig. 3, c). This implies that the humeral trochlea is cylindrical or cone shaped, and not the trochleiform shape characteristic of extant hominoids (Rose, 1993).

On the proximal shaft the area for the insertion of *m. brachialis* is well developed and deeply excavated as in hominoids, especially *Pan* (Fig. 3, d). There is a well developed ridge on the lateral surface, extending distally from the distoposterior corner of the radial notch (Fig. 3, e). This is for the origin of *m. supinator*, and the beginning of the interosseous border. The shaft is quite excavated posterior to this ridge (Fig. 3, f). As a result of these two features, the shaft is relatively mediolaterally broad in the region of the brachialis area and remains quite broad at the distal end of the brachialis area (Table 2, Index 1). These features are again most similar to those of extant hominoids. *Ateles* ulnae show similar metrical features but, morphologically, these are clearly due to a reduced anteroposterior dimension rather than an expanded mediolateral dimension. There is a distinct excavation on the medial side of the shaft, proximal to the brachialis insertion area and posterior to the distal part of the trochlear notch (Fig. 3, g). This is for the most proximal part of the origin of *m. flexor digitorum profundus* and possibly for an ulnar head of *m. pronator teres*. An excavated area is variably developed in this region in anthropoids, but the morphology of KNM-BG 17824 most resembles that on great ape ulnae.

Functional features: Among extant hominoids a trochleiform trochlea, together with the reciprocal morphology of the distal part of the ulnar trochlear notch, are part of a complex of features in the elbow region that provide a high degree of stability in the elbow region (Rose, 1988, 1993). In particular, the complex allows the humerus and ulna to lock together during rotatory movements of the body and forelimb below fixed handholds, especially suspensory activities (Sarmiento, 1985, 1988). While the indicators are minimal, the ulnar part of this complex is evidently lacking in KNM-BG 15071, and probably also in KNM-BG 17824. However, other features

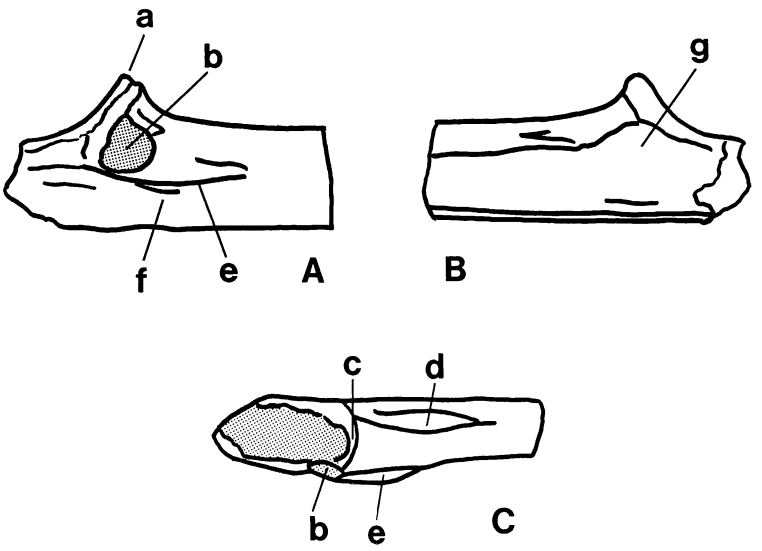

Figure 3. Morphological features of KNM-BG 17824 mentioned in the text. A, lateral; B, medial; and C, anterior views.

are more like those of extant hominoids. In these taxa, the presence of a protuberant, upright coronoid process is associated with an anteroproximal facing trochlear notch that is in turn associated with enhanced extension at the humeroulnar joint (Harrison, 1982; Sarmiento 1985, 1988; Rose, 1993). The presence of a well developed area for the insertion of *m. brachialis* is associated with powerful elbow flexion, and the orientation of the radial notch and the emphasized area of origin of *m. supinator* and possibly also of *m. pronator teres* indicate powerful and extensive pronation-supination movements of the forearm. Among extant taxa, particularly hominoids, all of the above functions are most commonly utilized during climbing behaviors.

Comparisons with other anthropoid fossil ulnae: A fairly transverse alignment of the distal border of the trochlear notch, suggested by the morphology of KNM-BG 15071, is characteristic of *Aegyptopithecus*, *Pliopithecus*, *Dendropithecus*, and *Proconsul* ulnae (Napier and Davis, 1959; Morbeck, 1975; Le Gros Clark and Thomas, 1951; Zapfe, 1960; Conroy, 1976). Ulnae of this type articulate with a cylindrical or cone shaped humeral trochlea bounded by an absent or only modestly developed lateral trochlear keel. This humeral morphology is also known for *Kenyapithecus wickeri* (Andrews and Walker, 1976; Senut, 1989). By contrast, the distal border of the trochlea notch is V-shaped in *Dryopithecus* (Morbeck, 1983; Begun, 1992), *Oreopithecus* (Harrison, 1986, 1991; Sarmiento, 1987), and extant hominoids, where it is associated with a more spool-shaped (i.e. truly trochleiform) humeral trochlea. An upright and relatively protuberant coronoid process, together with a laterally facing radial notch is present on the ulnae of *Dryopithecus* and *Oreopithecus*. A well

developed area for the insertion of *m. brachialis* is present on the ulnae of *Aegyptopithecus*, *Proconsul* (especially *nyanzae*) and *Dryopithecus*. KNM-BG 17824 is most similar to *Dryopithecus* in the detailed morphology of the area. A relatively well developed supinator crest is present in *Proconsul*, *Dryopithecus*, and *Oreopithecus*. An excavated area for *m. flexor digitorum profundus* and *m. pronator teres* is present on the ulnae, where known, of all the above mentioned taxa. Thus, unlike extant hominoids, *Dryopithecus*, and *Oreopithecus*, KNM-BG 15071 and 17824 lack the derived features associated with a fully trochleiform humeroulnar joint. However, they resemble those taxa in possessing derived features related to enhanced forearm rotation, powerful elbow flexion and, possibly, enhanced elbow extension.

Distal ends of metapodials KNM-BG 15541 and 17807

Introduction: KNM-BG 15541 is a 2.4 cm long partial metapodial preserving the distal shaft and head. The head is extensively eroded, and deformed by dorsoventral pressure. KNM-BG 17807 is a 1.7 cm distal metapodial end (Fig. 4). It is minimally eroded, but there is some deformation from dorsoventral pressure, mostly affecting the ventral part of the distal shaft and head. For the average of four dimensions (Fig. 5), the specimen is close to the mean for male *Papio* metatarsals and in the upper part of the range for male *Papio* metacarpals (Table 3, Size). Intraspecifically, anthropoid metatarsals are on average, mediolaterally narrower than the metacarpals, although there is usually some overlap in ranges. Also, in some species both the metatarsals and metatarsals may be broader than in other species. While this makes it difficult definitively to assess whether KNM-BG 17807 is a metatarsal or a

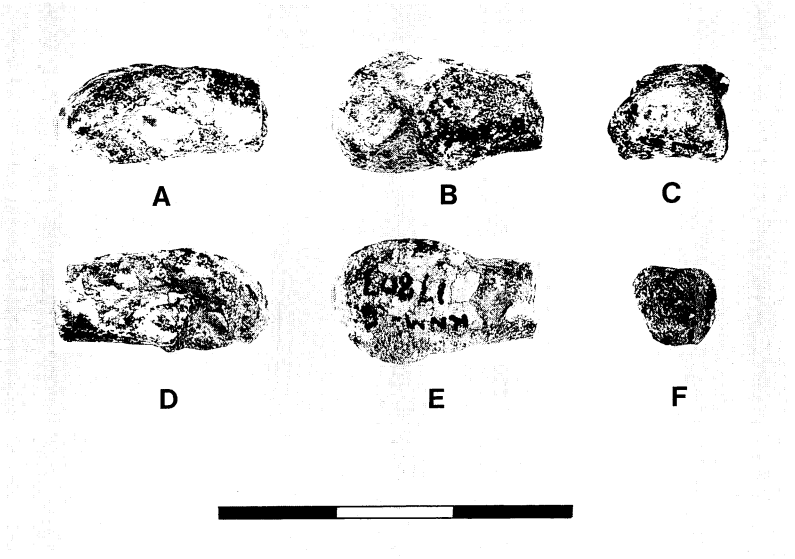

Figure 4. KNM-BG 17807 distal metapodial. A, left; B, dorsal; C, distal; D, right; and E, ventral views. F is the proximal cross section, with the dorsal surface towards the top of the page. Scale in cm.

metacarpal, its preserved morphology is more consistent with it being a metacarpal, and it will be assessed as such in what follows.

Description and functional features: The following description concentrates on the better preserved specimen, KNM-BG 17807. Using an estimated value for the dorsopalmar dimension, the distal shaft is apparently quite broad, to the degree found in *Cebus*, cercopithecid, and *Pan* metacarpals (Table 3, Index 1). Estimated proportions suggest that the head is relatively broad, as in *Cebus* and cercopithecids (Table 3, Index 2). The pits for the collateral ligaments of the metacarpophalangeal joint approximate the midline dorsally as in cebids and, especially, *Alouatta* (Fig. 6, a). The morphology of the palmar part of the head is equivocal due to the distortion. However, it is clear that there are well developed medial and lateral areas for articulation with the sesamoid bones (Fig. 6, b). There are no indications of grooves separating the sesamoid facets from a central area on the palmar part of the head ('fluting'-Lewis, 1989). Even in an undistorted specimen, this area between the sesamoid areas could not have been markedly protuberant (Fig. 6, c). In these features KNM-BG 17807 is most like *Cebus* and *Colobus* metacarpals. Specific indications as to function are not marked. The general similarities to cebids and cercopithecids suggests grasping hand use during predominantly pronograde quadrupedal activities. However, the specimen lacks the fluting of the palmar part of the head, associated with the functioning of the glenoid plate/sesamoid complex in essentially restricted flexion-extension movements (Lewis, 1989). This suggests a more versatile functioning of the metacarpophalangeal joint, although not to the degree seen in extant hominoids. This is also suggested by the placement of the pits for the collateral ligaments. The relatively dorsal, rather than medial or lateral, origin of the ligaments might permit more abduction-adduction and/or axial rotatory movements at the metacarpophalangeal joint without compromising their stabilizing function by becoming taut in full flexion. It suggests cheirideal involvement in activities other than stereotypical quadrupedalism.

Comparisons with other anthropoid fossil metacarpals: KNM-BG 17807 and the metacarpals of *Aegyptopithecus*, *Pliopithecus* (Zapfe, 1960), and *Proconsul* (Napier and Davis, 1959) share a similar morphology of the palmar part of the head. This morphology is less pronounced than that of many non-hominoid anthropoids, where there are well defined grooves for the passage of the sesamoid bones, separated by a pronounced midline keel. However the fossils also do not show the smoothing out of these features evident on extant large hominoid metacarpal heads, where the glenoid plate lacks associated sesamoids (Le Minor, 1988), and there are marked movement capabilities in more than one plane. The morphology of the fossil metacarpals is most consistent with a pattern of metacarpophalangeal movement that relies on the presence of a sesamoid bone/glenoid plate mechanism, but includes appreciable abduction- adduction, and possibly conjunct rotatory movements in addition to a flexion- extension capability. This in turn implies more than stereotyped hand grasping functions in association with varied positional activities. The morphology of the dorsal part of the head, in the region of the pits for the collateral ligaments of the metacarpophalangeal joint is shared by KNM-BG 17807, *Pliopithecus*, and *Proconsul* and has similar functional implications to the morphology of the plantar part of the head. A distal metacarpal of *Kenyapithecus africanus* from Maboko shares some fea-

Table 3. Metapodial indices and size comparisons.

	Index 1 Shaft proportions a×100/b[1]	Index 2 Head proportions c×100/d	Size a+b+c+d/4
Pan troglodytes[2] metacarpals[3]	115.0[4]	123.4	12.1
	95-135	107-148	9.8-14.0
	14.7	13.7	
Pan troglodytes metatarsals	70.5	153.3	9.9
	49-94	134-178	9.0-11.8
	13.9	14.8	
Hylobates spp. metacarpals	94.3	112.2	5.9
	60-97	60-82	5.2-6.8
	7.2	5.1	
Hylobates spp. metatarsals	77.6	136.9	5.1
	62-93	121-156	4.8-5.4
	8.8	12.5	
Papio cynocephalus metacarpals	—	—	7.2
Male			6.9-8.4
Papio cynocephalus metatarsals	—	—	7.9
Male			6.9-8.9
Cercopithecus mitis metacarpals	104.0	103.2	4.0
	87-122	95-109	3.2-4.6
	9.1	5.0	
Cercopithecus mitis metatarsals	105.6	106.4	4.8
	96-119	87-117	4.2-5.4
	7.3	10.8	
Colobus polykomos metacarpals	96.5	101.1	5.7
	85-109	92-108	4.6-6.8
	9.1	5.3	
Colobus polykomos metatarsals	95.7	108.5	6.5
	84-107	97-125	5.2-7.3
	7.6	7.6	
Ateles spp. metacarpals	88.6	122.6	6.2
	77-96	115-134	5.1-7.3
	5.6	5.0	
Ateles spp. metatarsals	74.0	137.4	6.0
	61-91	119-156	5.1-6.7
	9.6	14.6	
Cebus spp. metacarpals	107.2	107.6	4.1
	89-121	91-119	3.5-4.4
	10.1	8.9	
Cebus spp. metatarsals	94.1	119.0	4.4
	76-120	100-130	3.8-5.2
	15.6	10.5	
Kenyapithecus sp.[5]			
KNM-BG 17807	103.8	93.4	7.9
?*Aegyptopithecus zeuxis*			
DPC 1004 metacarpal 3	—	82.6	5.9
Pliopithecus vindobonensis			
Individual 3 metacarpal 2	85.9	113.3	6.0
Individual 3 metacarpal 3	99.1	95.0	6.4
Individual 3 metacarpal 4	100.4	98.5	6.3
Proconsul heseloni			
KNM-RU 2036E/J metacarpal 2	—	102.6	—
KNM-RU 2036G metacarpal 4	106.3	104.6	6.1
KNM-RU 2036H metacarpal 5	—	111.4	—
KNM-RU 2036BM metatarsal 2	85.9	—	—
KNM-RU 2036BN metatarsal 3	67.4	115.1	6.7
KNM-RU 2036BO metatarsal 4	84.0	—	—
?*Proconsul nyanzae*			
KNM-RU 1809 metapodial	108.1	104.1	9.7

[1] These are the measurements illustrated in Figure 5.
[2] $n=10$ for combined sex samples, $n=5$ for single sex samples.
[3] Metapodials are sampled from digits 2 through 5.
[4] Mean, range and S.D.
[5] Based on estimated measurements.

Figure 5. *Colobus polykomos* metacarpal in side (A) and dorsal (B) views, showing measurements taken (see also Table 3).

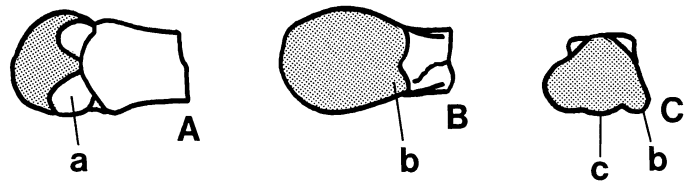

Figure 6. Morphological features of KNM-BG 17807 mentioned in the text. A, dorsal; B, ventral; and C, distal views.

tures with the Nachola specimens (McCrossin, 1994b; McCrossin and Benefit, 1995).

Femoral heads KNM-BG 15533, and 15536; heads with necks KNM-BG 17775, 17819, and 17821; proximal femora KNM-BG 17816 and 17820

Introduction: KNM-BG 15533 and 15536 are both partial, eroded femoral heads, with maximum dimensions of 1.8 cm and 1.5 cm respectively. KNM-BG 17775 is a 2.2 cm long femoral head and proximal neck, highly deformed by mediolaterally acting pressure. KNM-BG 17819 (Fig. 7, probably from the right side) and 17821 (probably from the left side) are both highly eroded heads with necks, and are 2.8 cm and 3.1 cm long respectively. KNM-BG 17816 (Fig. 7) and 17820 are right and left proximal femora, with maximum dimensions of 5.5 cm and 6.4 cm respectively. They are probably from the same individual. KNM-BG 17816 lacks the head, most of the neck, and the proximal and posterior parts of the greater trochanter. There is minor erosion on the lesser trochanter. Posteriorly, two fracture lines run from the base of the neck to the lesser and greater trochanters respectively. A slightly separated fracture runs straight down the anterior surface of the shaft. A longitudinal crack, with minor spreading of the bone, runs along the anteromedial surface, and another crack extends from the lesser trochanter to the base of the neck. KNM-BG 17820 is little more than a cracked and eroded shaft shorn of the head, neck, and trochanters. The head diameters listed in Table 4 are estimated or minimum values. KNM-BG 17816 and 17819 are similar in size to female *Papio* femora (Fig. 8; Table 4, Size 1 and Size 2). Visual inspection suggests that KNM-BG 17820 is also within this size range. The other specimens are similar in size to male *Papio* femora (Table 4, Head diameter, Size 1).

The following description is based mainly on the morphology of the least damaged specimens, KNM-BG 17816, 17819 (Fig. 7), and 17821. Because of erosion

Table 4. Femoral indices and size comparisons.

	Index 1 Neck proportions a×100/b[1]	Index 2 Neck/Shaft proportions c×100/d	Index 3 Shaft proportions d×100/e	Head diameter f	Size 1 a+b/2	Size 2 c+d+e/3
Pan troglodytes[2]	81.4[3]	82.8	81.2	31.5	19.6	21.8
	75-90	76-89	71-88	30.2-33.5	18.2-22.1	20.1-23.2
	4.6	4.3	4.5			
Hylobates spp.	79.2	84.8	83.8	16.1	9.2	9.8
	71-88	72-95	72-99	14.8-18.1	7.7-11.4	9.0-10.8
	5.6	8.1	9.5			
Papio cynocephalus	—	—	—	19.4	12.3	13.1
Female				18.2-20.5	10.9-13.4	11.4-14.5
Papio cynocephalus	—	—	—	23.3	15.6	16.3
Male				21.3-24.6	14.4-16.9	15.9-17.2
Cercopithecus mitis	72.7	77.5	105.5	12.5	8.7	8.4
	68-80	71-85	102-110	9.9-14.3	6.7-10.1	6.5-9.7
	3.4	4.3	2.5			
Colobus polykomos	71.7	83.4	93.7	16.3	11.9	11.3
	61-79	75-89	85-101	14.8-18.5	10.4-13.5	10.4-12.7
	5.2	3.6	5.2			
Ateles spp.	83.7	81.2	91.2	17.1	10.3	11.1
	78-91	75-91	85-97	15.0-19.9	8.4-13.0	10.0-13.5
	4.2	4.8	3.6			
Cebus spp.	77.1	72.6	94.9	11.0	7.1	7.9
	68-86	67-80	82-109	8.9-11.9	5.9-7.9	6.5-9.1
	5.5	4.3	9.0			
Kenyapithecus sp.						
KNM-BG 15533	—	—	—	23.6	—	—
KNM-BG 15536	—	—	—	21.1	—	—
KNM-BG 17775	—	—	—	21.2	—	—
KNM-BG 17816	—	87.7	84.9	—	—	14.9
KNM-BG 17819	79.6	—	—	19.0	13.2	—
KNM-BG 17820	—	—	81.0	—	—	—
KNM-BG 17821	73.1	—	—	21.9	13.8	—
?*Kenyapithecus africanus*						
BM M 16331	76.8	71.7	—	22.7	14.6	—
KNM-MB 12028	—	76.37	90.2	—	—	15.4
Pliopithecus vindobonensis						
Individual 2	76.2	89.1	81.4	17.6	11.1	11.8
?*Dendropithecus macinnesi*						
KNM-CA 2497, 2501; LG 1; RU 1640, 18388; SO 1964, 5123	—	—	—	16.1 15-18	—	—
KNM-RU 1636	—	71.6	87.9	—	—	10.9
Simiolus enjiessi						
KNM-WK 18117	83.8	83.2	81.7	10.6	6.8	8.0
?*Micropithecus* sp.						
KNM-WS 12636	—	87.9	85.4	—	—	—
?*Limnopithecus evansi*						
KNM-SO 1011	81.1	75.2	91.6	14.3	8.9	10.3
KNM-SO 5124	—	—	—	14.2	—	—
?*Limnopithecus legetet*						
KNM-RU 7694	73.4	78.8	81.7	13.5	8.1	8.6
?*Rangwapithecus gordoni*						
KNM-SO 399	75.1	73.6	78.9	21.4	14.2	14.6
Proconsul heseloni						
KNM-RU 3086	—	—	—	20.1	—	—
KNM-RU 2036CL	—	80.5	85.5	—	—	12.1
Proconsul nyanzae						
KNM-MW 13142; RU 1633, 1753 5527, 5950	—	—	—	26.8 25.3-30.0	—	—
KNM-MW 13142	76.0	80.8	83.8	—	17.4	19.6
KNM-RU 1753	87.3	—	—	—	19.4	—
KNM-RU 3688	—	83.0	78.7	—	—	21.7
KNM-RU 5527	71.9	—	—	—	16.4	—
KNM-RU 17379	—	78.8	88.6	—	—	—
Sivapithecus indicus						
GSP 6178, 11869, 13929	—	—	24.8 24-26	—	—	—
GSP 12654	68.1	—	—	—	13.7	—

[1] These are the measurements illustrated in Figure 8.
[2] $n=10$ for combined sex samples, $n=5$ for male and female samples.
[3] Mean, range and S.D.

around the margins of the head it is not possible to determine the extent of encroachment onto the neck of the articular surface. The neck is anteroposteriorly compressed to the extent seen in most extant anthropoids (Fig. 8, Table 4, Index 1). On KNM-BG 17821 the remains of a tubercle of the neck is present on the superior part of the posterior surface of the neck. Such a tubercle is found on the necks of many non-hominoid primates. Compared to the anteroposterior diameter of the proximal shaft, the neck is as anteroposteriorly deep as in extant anthropoids other than *Cercopithecus* and *Cebus* (Table 4, Index 2). In proximal view the trochanteric fossa (Fig. 9, a) is bounded by anterior and posterior ridges (Fig. 9, b and c). In posterior view the posterior ridge is placed considerably more distally than the anterior ridge, although it is nevertheless strongly developed. This morphology is similar to extant hominoid femora. In other extant anthropoids the posterior ridge is minimally developed, and the trochanteric fossa is thus open posteriorly.

The only distinctive feature preserved on the greater trochanter is the proximal part of a protuberant lateral surface (Fig. 9, d). This feature is found on the femora of cercopithecids and hylobatids. While the greater trochanter may be somewhat laterally projecting in some *Pan* specimens, the insertion area for the lesser gluteal muscles is anteroposteriorly deeper than in the other taxa. A discrete and protuberant gluteal tuberosity is placed relatively proximally on the border between the posterior and lateral surfaces, so that the distance between it and the greater trochanter is relatively short (Fig. 9, e). The combination of greater trochanter and gluteal tuberosity features is most similar to the condition in cercopithecids and hylobatids.

The lesser trochanter is well developed and projects more laterally than it does posteriorly, so that it is completely visible in anterior view (Fig. 7A; Fig. 9, f). This most resembles the condition in hylobatids and *Ateles* among extant anthropoids. A distinct intertrochanteric crest runs obliquely across the posterior surface between the two trochanters (Fig. 9, g). Proximal to this the base of the neck is somewhat excavated (Fig. 9, h). The proximal shaft is relatively compressed anteroposteriorly (Table 4, Index 3), and most resembles the condition in extant hominoid femora.

Function: The most distinctive features of KNM-BG 17816 and 17820 are the emphasized lateral surface of the greater trochanter, the size and positioning of the gluteal tuberosity, and the size and positioning of the lesser trochanter. These features imply that both the lesser and greater gluteal muscles may have been well developed and, with respect to the lesser gluteals, may have acted as rotators as well as extensors. The hindlimb may thus have been held in a partial external rotation, with the knee semi-flexed and pointing somewhat laterally. Such a position is most likely to have been utilized during both quadrupedal locomotion and during climbing, as has been documented for *Pan* (Fleagle *et al.*, 1981). The similarities between the femora of *Nasalis* and *Kenyapithecus africanus* femora from Maboko Island (McHenry and Corruccini, 1976) is consistent with this interpretation.

Comparisons with other catarrhine fossil femora: In all comparable features the Nachola *Kenyapithecus* femoral specimens are closely similar to those of *Kenyapithecus africanus* from Maboko Island (Le Gros Clark and Leakey, 1951), although the Nachola specimens are slightly smaller in size (Table 4, Size 1 and Size 2). All of these specimens are in turn quite similar to those of *Proconsul*. Major similarities between the *Kenyapithecus* specimens and *Proconsul* femora include the morphology

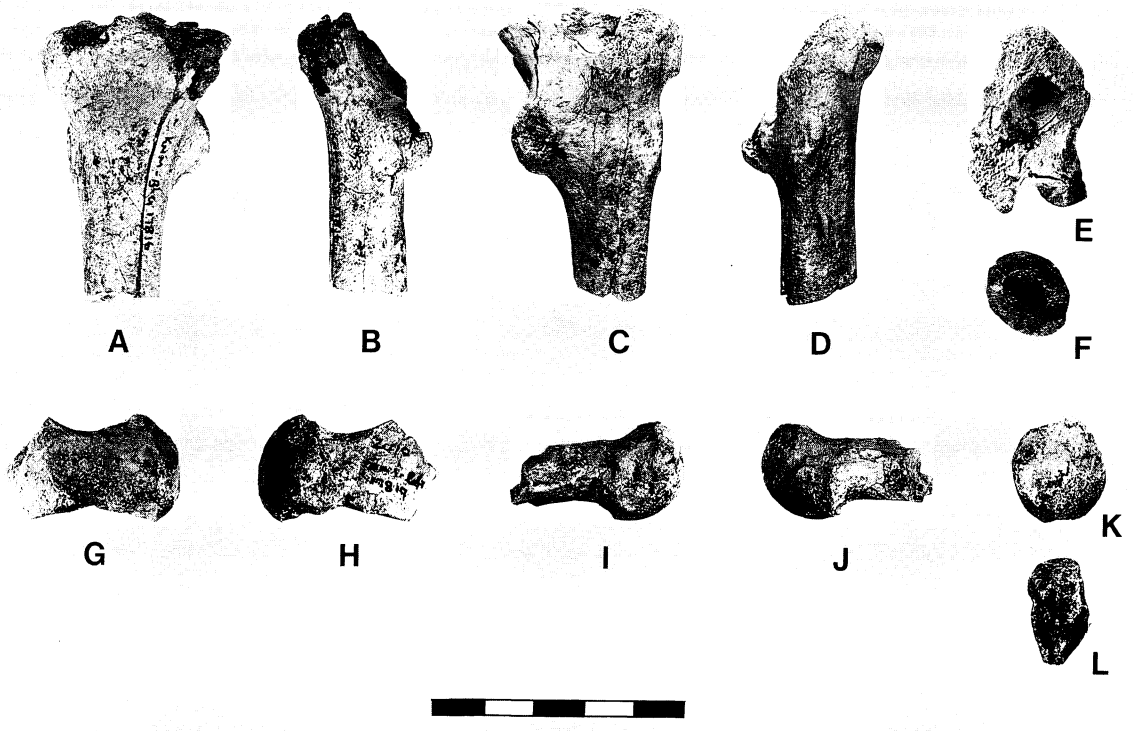

Figure 7. KNM-BG 17816 right femur. A, anterior; B, medial; C, posterior; D, lateral; and E, proximal views. F is the distal cross section. Lateral is towards the top of the page in E and F. KNM-BG 17819 right femur. G, anterior; H, posterior; I, distal; J, proximal; K, medial views. L is the lateral cross section. Proximal is towards the top of the page in K and L. Scale in cm.

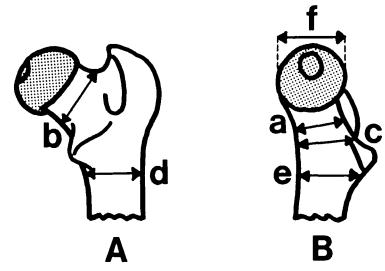

Figure 8. *Colobus polykomos* right femur in posterior (A) and medial (B) views, showing measurements taken (see also Table 4).

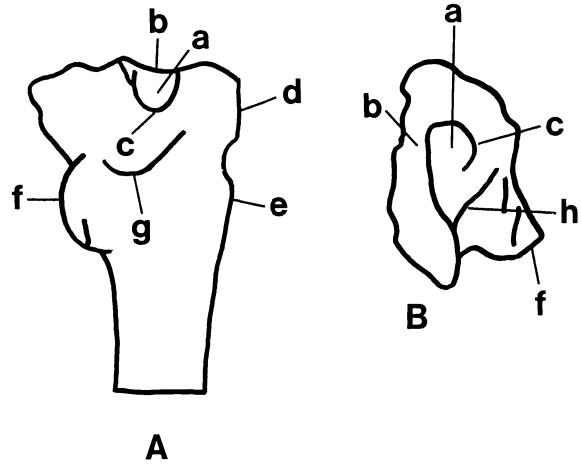

Figure 9. Morphological features of KNM-BG 17816 mentioned in the text. A, posterior and B, proximal views.

of the greater trochanter, the partial closure of the trochanteric fossa by a posterior buttress, and the presence of a tubercle of the neck. However, in the *Kenyapithecus* specimens the neck is apparently somewhat shorter than in *Proconsul*, the lesser trochanter is more medially directed, there is a relatively shorter distance between the gluteal tuberosity and the greater trochanter, and the proximal shaft is more gracile. All of these similarities to, and differences from *Proconsul* are also shown by the Maboko *K. africanus* specimens. The shortness of the neck and the gracility of the shaft are particularly evident in the Maboko specimens. The femora of all the above taxa differ from those of *Simiolus* (Rose *et al.*, 1992) and other small apes in having a more robust neck and a well developed buttress posterior to the trochanteric fossa. The femur of *Pliopithecus* resembles the *Kenyapithecus* specimens in the morphology of the greater and lesser trochanters (Zapfe, 1960). It also possesses a

Table 5. Patellar indices and size comparisons.

	Index 1 Width/length b×100/a[1]	Index 2 Articular length c×100/a	Index 3 Depth/width d×100/b	Index 4 Depth/length d×100/a	Index 5 Articular proportions c×100/b	Index 6 Articular curvature (d-e)×100/c	Size (a+b+d)/3
Pan troglodytes[2]	100.7[3]	85.4	42.4	42.7	85.2	2.7	21.9
	83-106	79-96	37-49	34-50	75-101	1-5	20.2-24.1
	7.7	5.4	4.3	5.1	8.5	1.4	
Hylobates spp.	83.5	82.6	44.0	36.7	99.7	7.0	12.6
	74-90	71-93	40-50	32-40	86-124	5-11	11.4-14.3
	6.4	5.8	2.4	3.0	12.8	1.9	
Papio cynocephalus	—	—	—	—	—	—	14.4
Female							14.0-15.8
Cercopithecus mitis	69.5	69.2	65.4	45.4	100.0	6.6	10.9
	61-81	61-80	62-73	41-53	80-123	5-9	8.3-14.0
	5.6	6.3	3.4	3.2	11.8	1.2	
Colobus polykomos	67.7	68.4	64.3	43.5	101.3	7.0	13.7
	59-75	59-78	58-71	40-50	82-113	5-9	12.1-16.2
	4.7	5.7	4.9	3.2	9.4	1.3	
Ateles spp.	80.4	80.7	51.4	41.2	101.5	5.7	13.5
	68-91	73-89	47-55	35-47	80-119	2-9	11.2-16.4
	7.5	4.6	2.6	3.9	14.0	2.7	
Cebus spp.	77.7	71.9	54.3	41.8	93.1	4.5	9.7
	68-95	64-81	47-66	38-45	78-104	3-8	7.4-11.6
	8.4	4.9	6.2	2.4	7.7	2.0	
Kenyapithecus sp.							
KNM-BG 15535	98.0	79.4	38.0	37.2	81.0	4.4	15.6
Pliopithecus vindobonensis							
Individual 2	88.2	85.9	40.0	35.3	97.3	5.7	12.7
Proconsul heseloni							
KNM PT 2[4]	89.0	87.1	31.9	—	97.8	—	—
KNM PT 3	96.1	77.7	34.5	33.1	80.8	1.3	11.7
KNM PT 4	96.2	88.9	40.6	39.1	92.3	2.4	11.6
Proconsul nyanzae							
KNM-RU 17382	88.0	—	45.6	40.1	—	—	19.5
KNM-RU 18384	88.7	—	46.6	41.3	—	—	20.4
Indet. ?hominoid							
KNM-CA 406	—	—	35.9	—	—	—	—

[1] These are the measurements illustrated in Figure 11.

[2] $n=10$ for combined sex samples, $n=5$ for the single sex sample.

[3] Mean, range and S.D.

[4] Temporary identifications for unaccessioned specimens.

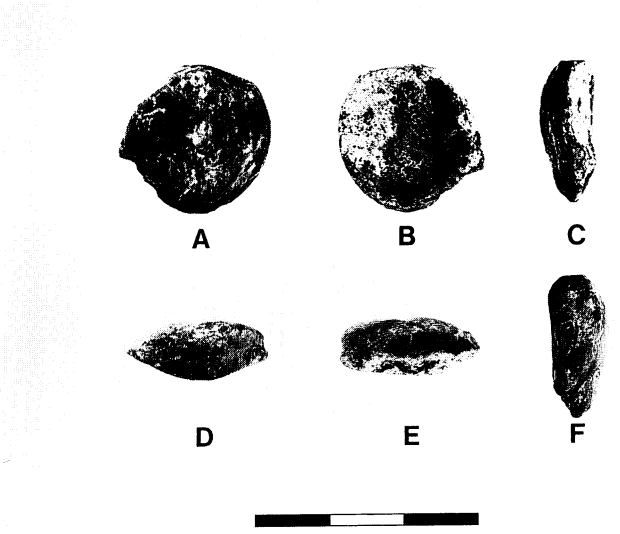

Figure 10. KNM-BG 15535 left patella. A, anterior; B, posterior; C, lateral; D, proximal; E, distal; and F, medial views. Scale in cm.

tubercle of the neck, and a modestly developed posterior buttress to the trochanteric fossa. However, in *Pliopithecus*, both the neck and proximal shaft are more gracile than in *Kenyapithecus*.

Left patella, KNM-BG 15535

Description: KNM-BG 15535 is a complete, uneroded left patella, approximately 2 cm long proximodistally (Fig. 10). For the average of three dimensions, KNM-BG 15535 falls within the upper part of the range for female *Papio* patellae (Fig. 11; Table 5, Size). The proximal half of the specimen is semicircular in outline, while the distal half is more tapered. However, the bone is almost equal in its proximodistal and mediolateral dimensions (Table 5, Index 1). This results from an abbreviated non-articular distal area that serves as the origin for the patellar tendon (Fig. 12, a; Table 5, Index 2). It is anteroposteriorly shallow, especially compared to its mediolateral diameter (Table 5, Index 3) but also compared to its proximodistal diameter (Table 5, Index 4). The maximum anteroposterior dimension is situated proximally. In all these features KNM-BG 15535 most resembles *Pan*. The articular area itself is somewhat elongated mediolaterally (Table 5, Index 5), more so than in most anthropoid patellae except those of *Pan*. In medial or lateral view the articular surface is slightly concave, to the extent seen in *Pan* and platyrrhine patellae (Fig. 12, b; Table 5, Index 6). The surface is mildly convex in proximal or distal view (Fig. 12, c), with a longer and less curved medial portion.

Function: The morphology of KNM-BG 15535 most resembles the patellae of *Pan*, but is also quite similar to those of *Ateles* and *Cebus*. The patella is attached to the tibia via a broad patellar ligament, and evidently articulates with a femoral patel-

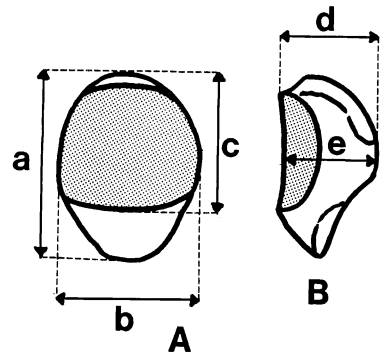

Figure 11. *Colobus polykomos* left patella in posterior (A) and medial (B) views, showing measurements taken (see also Table 5).

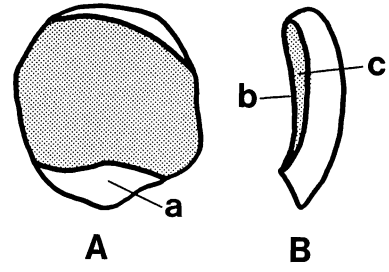

Figure 12. Morphological features of KNM-BG 15535 mentioned in the text. A, posterior and B, medial views.

lar groove that is relatively broad mediolaterally and relatively shallow anteroposteriorly. This may imply that the distal femur as a whole is relatively broad. This configuration is strikingly different to the patellofemoral joint in cercopithecids, where a narrow, deep patella, with a highly curved articular surface, rides within a similarly deep and narrow patellar groove on the femur. The shallower, saddled type of joint in KNM-BG 15535 and extant hominoids, may provide a capability for rotation of the patella around an anteroposterior axis, either conjunct or adjunct to the movement of the patella during flexion-extension of the knee, or as a result of axial rotation of the femur on the tibia. Conjunct patellar rotation has been documented for the human knee. Medial rotation is maximal in flexion combined with lateral rotation of the femur on the tibia (Kampen & Huiskes, 1990). Adjunct rotation might occur as a result of the differential contraction of, especially, *m. vastus medialis* and *m. vastus lateralis*. In non-human hominoids both conjunct and adjunct patellar rotation would be particularly important during extension of the eccentrically loaded knee in activities such as clambering and climbing.

Comparisons with other catarrhine fossil patellae: KNM-BG 15535 is similar to a

patella of *Kenyapithecus africanus* from Maboko (McCrossin 1994b; McCrossin and Benefit, 1995). KNM-BG 15535 is generally similar to the patellae of the fossil catarrhines *Pliopithecus vindobonensis* (Zapfe, 1960), and *Proconsul heseloni* and *P. nyanzae* (Ward *et al.*, 1995). These patellae resemble KNM-BG 15535 in being anteroposteriorly shallow. They are relatively a little longer and, in the case of *Pliopithecus* the articular surface is slightly more curved, although not to the extent seen in cercopithecids. Ward *et al.* (1995) suggest that it is the anteroposterior shallowness of these patellae that is their most significant functional feature. It indicates that in these taxa the patella is not stressed to the extent found in running and leaping primates. Ward *et al.* (1995) also suggest that a disc-shaped, shallow patella is probably the primitive state for hominoids. The similarities described above among KNM-BG 15535, *Pliopithecus*, and (to a certain extent) cebids suggests that this condition might also be primitive for catarrhines.

Right distal fibulae KNM-BG 17809 and 17810

Introduction: KNM-BG 17809 is 3.4 cm long proximodistally and consists of the most distal part of the shaft together with the articular and malleolar regions. The end of the bone is extensively eroded, apart from a portion of the facet that articulates with the lateral side of the talus. KNM-BG 17810 is a 2.8 cm long fragment that preserves the distal end (Fig. 13). It is free from erosion or distortion. For the average of four measurements of the distal end, the specimen is the same size as large male *Papio* fibulae (Fig. 14; Table 6, Size). As KNM-BG 17809 is undamaged,

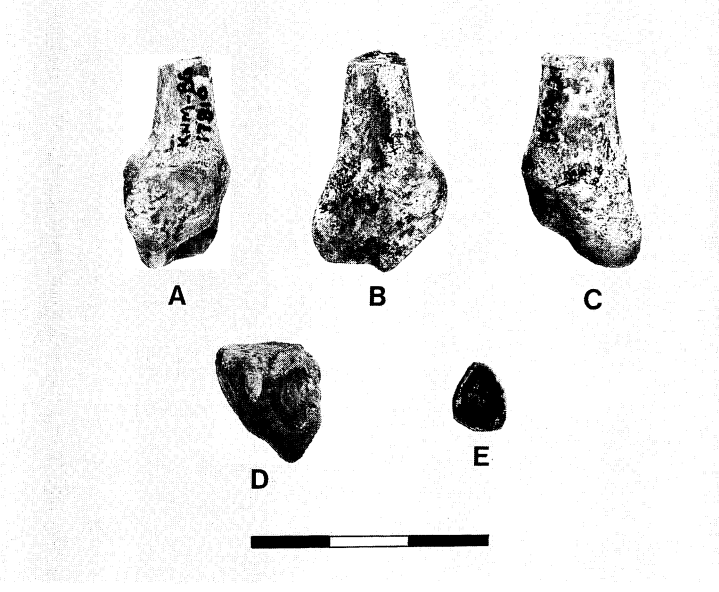

Figure 13. KNM-BG 17809 right fibula. A, medial; B, anterolateral; C, posterior; and D, distal views. E is the proximal cross section. Medial (D) and posterior (E) are towards the top of the page. Scale in cm.

it forms the basis for the following description.

Description: The distal shaft is roughly triangular in cross section, with a distinct lateral border and more rounded anteromedial and posteromedial borders (Fig. 13). It is compressed mediolaterally (Table 6, Index 1), to the degree seen in non-cercopithecid anthropoids. The distal end is expanded mediolaterally as in extant hominoids and *Ateles* (Table 6, Index 2). On the medial aspect of the distal end, the facet for the lateral side of the talus (Fig. 15, a) slants posteroproximally to anterodistally, as in all anthropoids. It is deep proximodistally, as in extant hominoids, and faces

Table 6. Fibular indices and size comparisons

	Index 1 Distal shaft proportions	Index 2 Depth/width distal end	Index 3 Length/depth facet for lateral talus	Index 4 Width/depth facet for talar lateral process	Index 5 Ligament area proportions	Size	Facet Angle
	a×100/b[1]	c×100/d	e×100/f	g×100/h	i×100/c	(c+d+j+k)/4	l
Pan troglodytes[2]	90.1[3]	78.1	67.4	69.3	88.0	21.3	63.4
	72-99	68-91	52-84	42-86	80-101	19.8-22.9	55-70
	8.3	7.5	10.9	13.01	8.4		4.5
Hylobates spp.	77.2	79.3	68.5	76.9	93.0	9.5	63.6
	66-95	69-95	56-79	62-93	79-105	8.2-10.7	55-73
	8.2	7.8	8.1	9.9	8.1		6.5
Papio cynocephalus	—	—	—	—	—	13.6	—
Male						13.2-14.7	
Cercopithecus mitis	90.8	119.1	66.2	81.4	73.8	7.8	86.4
	78-99	108-138	60-71	58-99	56-87	6.6-9.1	77-90
	6.7	10.1	3.8	14.7	9.6		3.9
Colobus polykomos	91.8	110.1	54.9	71.2	76.1	10.3	81.9
	81-100	93-127	42-69	58-96	67-87	9.1-11.7	74-88
	6.0	11.1	9.5	11.5	7.3		4.0
Ateles spp.	83.1	92.7	52.7	68.7	84.3	11.3	66.7
	69-96	77-106	42-78	57-80	71-95	9.7-12.9	55-72
	9.3	8.3	10.4	8.4	7.5		4.8
Cebus spp.	79.5	102.8	60.5	85.3	79.6	7.9	79.2
	66-95	90-114	52-68	73-106	65-90	6.8-8.9	75-84
	7.8	8.7	5.2	12.9	6.5		3.6
Kenyapithecus sp. KNM-BG 17810	75.0	83.1	78.1	56.1	92.3	14.3	73
Proconsul heseloni KNM FB 5[4]	—	109.7	69.9	76.8	64.4	11.3	68
?*Proconsul africanus* KNM-CA 1834	—	98.2	59.2	63.2	78.0	12.9	61
Proconsul nyanzae KNM-MW 13142	83.2	78.6	60.7	85.2	71.1	19.2	60

[1] These are the measurements illustrated in Figure 14.

[2] $n=10$ for combined sex samples, $n=5$ for the single sex sample.

[3] Mean, range and S.D.

[4] Temporary identification for unaccessioned specimen.

mediodistally, as in extant hominoids and *Ateles* (Table 6, Index 3, Facet Angle). Contiguous with the anterior part of the distal border of this facet is a triangular facet for articulation with the lateral process of the talus (Fig. 15, b). This is slightly longer anteroposteriorly than is usual in anthropoids other than *Pan* (Table 6, Index 4). Extending proximally from the proximal border of the facet for the lateral side of the talus are a small anterior facet and an even smaller posterior facet that extend into the region of the otherwise poorly demarcated tibiofibular syndesmosis (Fig. 15, c and d). This again resembles the condition in extant hominoids.

A smooth, posterodistally facing area is present on the posterior surface, adjacent to the posterior margin of the facet for the lateral side of the talus (Fig. 15, e). An area of this type occurs in large extant hominoids and is associated with the attachment of the posterior tibiofibular ligament. The fibular malleolus is fairly robust and a moderately excavated area for the attachment of the talofibular and calcaneofibular ligaments is present between it and the region of the articular facets (Fig. 15, f). This area is relatively broad, as in extant hominoids and *Ateles*, and provides a large area for the attachment of the ligaments (Table 6, Index 5).

Function and comparisons with other hominoid fossil fibulae: In most of its functional features, KNM-BG 17810 resembles the distal fibulae of extant hominoids, particularly African apes. The presence of synovial components in the otherwise syndesmotic distal tibiofibular joint may reflect an enhanced capability of the fibula to axially rotate and move posteriorly together with the talus, and on the tibia, as the talocrural joint moves into a dorsiflexed and abducted position. This is known to occur in the human ankle joint (Svensson *et al.*, 1989). The angulation of the facet for the lateral side of the talus, in combination with a somewhat distolaterally facing facet on the tibia, results in the talus having an eversion set within the talocrural

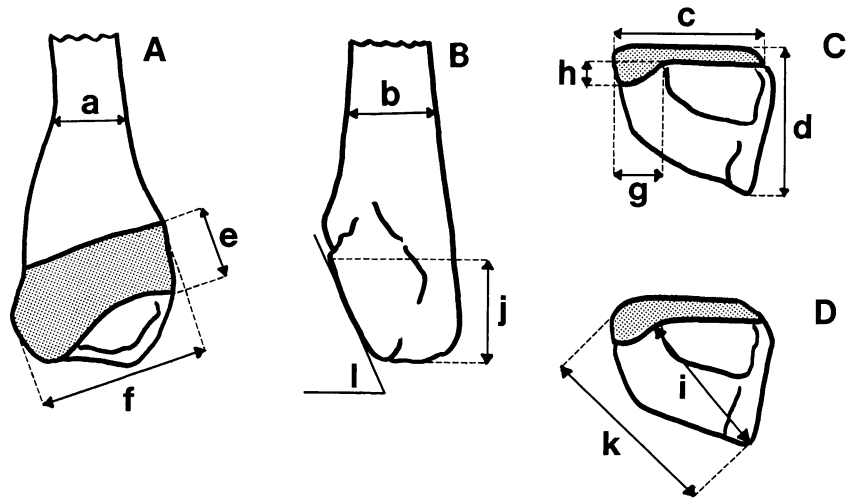

Figure 14. *Colobus polykomos* right fibula in medial (A), posterior (B), and distal (C and D) views, showing measurements taken (see also Table 6).

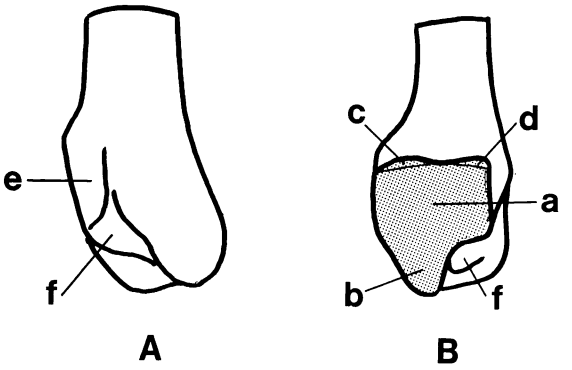

Figure 15. Morphological features of KNM-BG 17809 mentioned in the text. A, posterior and B, medial views.

joint. However, the talus regains a more horizontal position to the extent that the hip joint is externally rotated and the knee joint is flexed, as occurs especially during climbing. From this position further movements within the ankle and foot may serve to bring the plantar surface of the foot into contact with a vertical support. The set of the talus within the tibiofibular mortise is also associated with an anteroposteriorly long lateral process of the talus and corresponding facet on the fibula, and with an extensive fibular attachment area for the talofibular and calcaneofibular ligaments. The fibular morphology of KNM-BG 17810 is consistent with that of an animal that, like African apes, combines quadrupedalism with vertical climbing. A distal fibula of *Kenyapithecus africanus* from Maboko is similar to KNM-BG 17810, especially in the orientation of the facet for the lateral side of the talus (McCrossin and Benefit, 1995). *Proconsul* distal fibulae are quite similar to KNM-BG 17810 in all essential features of their functional morphology.

Partial right talus KNM-BG 15529

Introduction: KNM-BG 15529 is an eroded right talar trochlea, approximately 2 cm long proximodistally (Fig. 16). The head and most of the neck are missing and there is erosion around the proximal end of the trochlear articular surface and around the articular surface for the proximal talocalcaneal joint. The medial side of the trochlea is slightly eroded, and punctured by a number of tooth marks. For the average of three measurements KNM-BG 15529 is close to the mean value for male *Papio* tali (Fig. 17; Table 7, Size). Although they are from different sites, KNM-BG 15529 makes a close fit with the fibula KNM-BG 17810.

Description, function, and comparisons with other catarrhine fossil specimens: The trochlea surface is somewhat lower on the medial side than on the lateral side and the trochlear groove is moderately developed (Fig. 18, a, b). The trochlea is relatively broad for its length, as in extant hominoids (Table 7, Index 1). On the lateral side the trochlea is as deep as is normal for anthropoids (Table 7, Index 2). In dorsal view the distal half of the trochlea is square sided, as in extant hominoids (Table 7, Index 3), although it is not possible to tell whether or not the trochlea as a whole is

Table 7. Talar indices and size comparisons

	Index 1 Trochlear proportions in dorsal view a×100/b[1]	Index 2 Trochlear proportions in lateral view c×100/b	Index 3 Trochlear wedging d×100/a	Index 4 Lateral/medial neck proportions c×100/e	Size (a+c+f)/3
Pan troglodytes[2]	80.9[3]	57.7	96.5	106.1	20.3
	73-88	49-69	90-103	86-126	18.6-22.2
	5.2	6.2	3.9	13.3	
Hylobates spp.	73.0	52.8	91.6	96.9	9.8
	68-80	46-62	85-100	74-117	8.8-11.4
	3.6	5.5	4.9	13.6	
Papio cynocephalus	—	—	—	—	15.5
Male					14.8-16.4
Cercopithecus mitis	78.8	60.0	96.8	89.2	9.3
	75-84	54-70	93-100	73-100	7.8-11.0
	3.4	5.1	2.2	7.9	
Colobus polykomos	88.5	58.9	93.7	109.2	12.1
	80-97	52-68	87-97	89-135	10.5-13.4
	4.8	5.3	3.5	14.1	
Ateles spp.	98.7	44.5	81.7	124.5	13.0
	92-105	36-56	77-88	107-144	12.0-14.0
	4.2	6.6	3.4	12.5	
Cebus spp.	82.7	56.1	92.6	97.3	8.5
	77-88	50-65	89-96	79-105	7.2-9.8
	3.4	4.1	2.4	7.2	
Kenyapithecus sp.	75.7	56.9	98.8		15.7
KNM-BG 15529					
Aegyptopithecus zeuxis	82.3	49.7	98.1	100.0	8.7
DPC 1301					
Pliopithecus vindobonensis	70.8	50.6	91.6	109.4	11.7
Individual 1					
?*Dendropithecus macinnesi*					
KNM-RU 1748	71.1	50.6	102.3	107.5	10.6
KNM-RU 5945	—	—	96.9	96.8	—
?*Kalepithecus songhorensis*					
KNM-SO 478	80.5	60.8	89.9	106.9	11.2
KNM-SO 967	75.6	58.2	94.4	83.0	10.9
?*Limnopithecus evansi*	79.3	55.5	89.2	100.4	8.6
KNM-SO 392					
?*Limnopithecus legetet*	70.3	55.7	103.6	94.3	—
KNM-LG 621					
Simiolus enjiessi	—	—	91.8	85.3	10.4
KNM-WK 17171A					
?*Rangwapithecus gordoni*					
KNM-SO 966	—	—	88.3	—	—
KNM-SO 968	—	—	98.9	81.0	—
Proconsul heseloni	74.4	58.7	97.2	95.2	12.7
KNM-RU 1744, 1745,	70-81	53-63	93-103	87-101	11.5-13.6
2036CO & BF, 14187	4.1	4.1	4.4	6.1	
Proconsul nyanzae	74.3	55.8	101.1	96.1	20.5
KNM-RU 1743, 1896, 5940,	67-79	52-59	96-108	90-104	19.0-20.5
& KNM-MW 13142C	5.4	3.3	5.1	5.6	
Proconsul major	74.2	58.2	98.2	94.3	22.8
KNM-SO 389					

[1] These are the measurements illustrated in Figure 17.
[2] $n=10$ for combined sex samples, $n=5$ for the single sex sample.
[3] Mean, range and S.D.

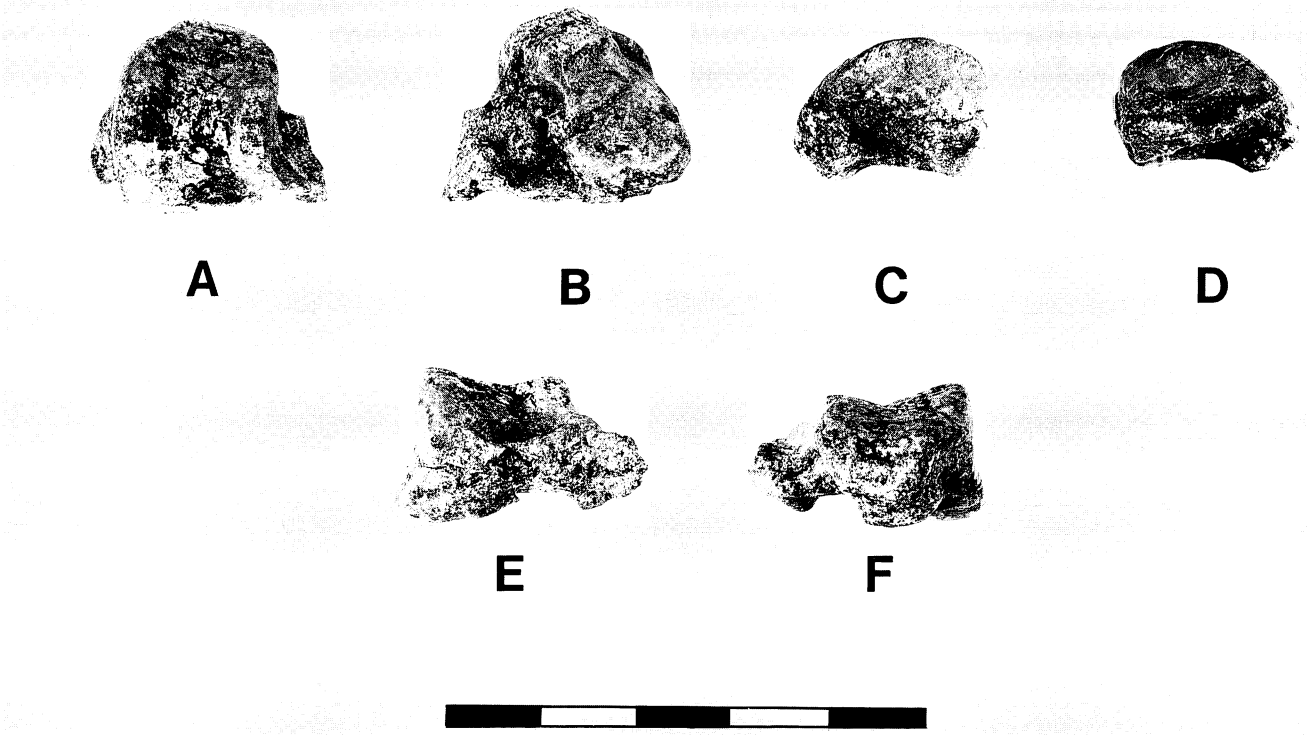

Figure 16. KNM-BG 15529 right talus. A, dorsal; B, plantar; C, lateral; D, medial; E, distal; and F, proximal views. Scale in cm.

wedged, due to erosion proximally. Medially, the base of the neck is apparently quite dorsoplantarly shallow (Table 7, Index 4). The articular surface for the proximal talocalcaneal joint is somewhat distorted, as well as being eroded around its edges, and no clear estimate of its degree of curvature can be determined (Fig. 18, c). A shallow *sinus tali* separates this surface from the surface for the distal talocalcaneal joint (Fig. 18, d). Only the most proximal part of the latter surface is preserved (Fig. 18, e). The trochlear morphology of a talus of *Kenyapithecus africanus* from Maboko is similar to that of KNM-BG 15529 (McCrossin, 1994b; McCrossin and Benefit, 1995). In its preserved parts, KNM-BG 15529 is quite similar to the tali of other large bodied Miocene hominoids. While talar morphology in these taxa is not closely similar to that of any particular extant taxon, there are eclectic similarities to the tali of large bodied platyrrhines and hominoids. It indicates function in the ankle region that is not as constrained as in cercopithecids or in specialized leaping primates.

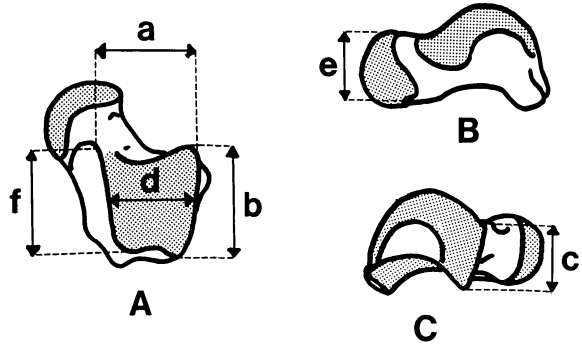

Figure 17. *Colobus polykomos* right talus in dorsal (A), medial (B), and lateral (C) views, showing measurements taken (see also Table 7).

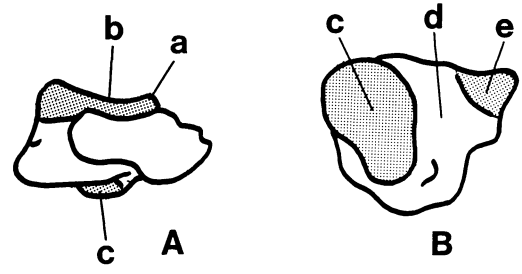

Figure 18. Morphological features of KNM-BG 15529 mentioned in the text. A, distal and B, plantar views.

Table 8. Calcaneal indices and size comparisons

	Index 1 Distal segment proportions	Index 2 Distal surface proportions	Index 3 Relative depth	Index 4 Minimum/ maximum depth	Proximal facet angle	Size
	a×100/b[1]	c×100/a	d×100/b	e×100/d	f	(a+b+d)/3
Pan troglodytes[2]	57.9[3]	83.7	74.8	56.2	39.5	27.5
	53-70	71-98	69-85	43-70	30-46	23.1-29.9
	4.0	7.3	4.3	6.3	4.8	
Hylobates spp.	56.2	73.1	66.2	57.0	18.3	13.7
	47-64	65-83	52-82	46-70	11-28	11.7-16.9
	5.1	4.6	6.4	7.4	4.4	
Papio cynocephalus	—	—	—	—	—	22.9
Male						21.8-24.4
Cercopithecus mitis	44.3	84.4	59.5	56.9	18.9	13.5
	42-47	75-100	54.8	51-64	14-24	11.0-15.2
	2.0	7.7	3.3	3.5	3.8	
Colobus polykomos	46.5	87.1	62.2	63.8	18.7	18.2
	41-51	80-94	58-69	56-71	13-25	15.9-20.2
	3.4	4.9	3.7	5.7	3.9	
Ateles spp.	42.8	83.8	54.5	51.6	15.8	18.8
	39-46	75-90	49-59	45-60	12-20	17.8-20.5
	2.4	5.6	4.2	4.5	2.7	
Cebus spp.	46.8	75.3	52.2	56.2	13.8	12.9
	40-51	69-87	48-55	49-66	5-25	11.6-14.3
	3.0	5.4	2.4	5.2	6.4	
Kenyapithecus sp.	46.9	66.2	51.2	48.1	22	22.3
KNM-BG 17805						
Pliopithecus vindobonensis	45.9	79.1	56.8	48.6	16	18.5
Individual 1						
?*Dendropithecus macinnesi*						
KNM-RU 1659	48.6	69.7	56.3	52.4	14	18.3
KNM-RU 1660	49.1	74.0	55.6	55.9	13	17.5
?*Limnopithecus legetet*	48.5	69.1	58.1	54.9	20	13.6
KNM-CA 2270						
?*Rangwapithecus gordoni*	56.0	81.8	—	—	—	—
KNM-SO 427						
Proconsul heseloni						
KNM-RU 1755	—	70.6	—	55.5	—	—
KNM-RU 2036BG	—	75.3	—	65.0	19	—
KNM-RU 2036CP	45.9	72.5	57.3	54.7	21	18.2
Proconsul nyanzae						
KNM-RU 5872F	—	73.7	—	59.1	14	—
KNM-MW 13142B	58.3	79.6	69.4	47.1	21	27.9
Proconsul major	52.1	75.7	73.5	50.8	24	33.2
KNM-SO 390						
Sivapithecus parvada						
GSP 17152	50.8	85.6	65.3	48.4	23	33.0
GSP 17606	60.0	86.8	68.8	53.1	27	28.4

[1] These are the measurements illustrated in Figure 20.

[2] $n=10$ for combined sex samples, $n=5$ for the single sex sample.

[3] Mean, range and S.D.

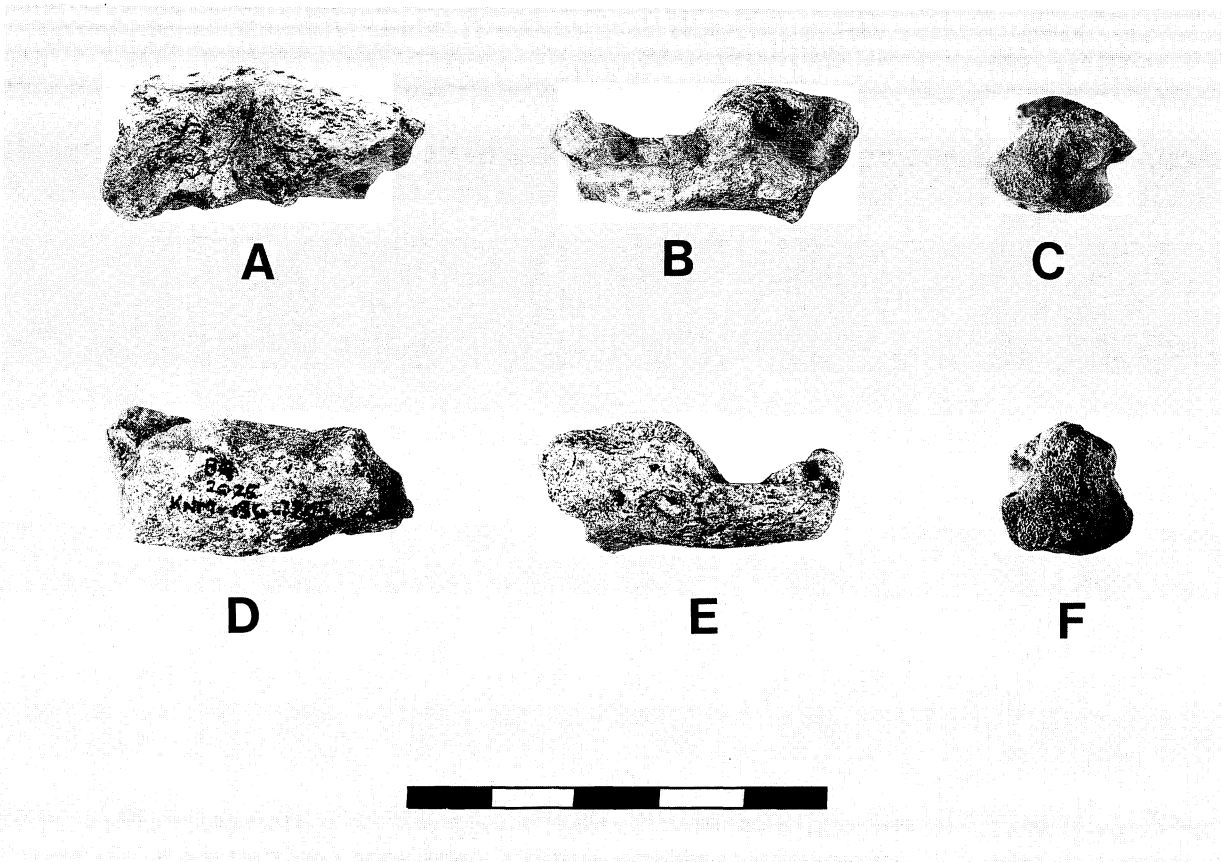

Figure 19. KNM-BG 17805 right calcaneus. A, dorsal; B, medial; C, distal; D, plantar; E, lateral; and F, proximal views. Scale in cm.

Partial right calcaneus KNM-BG 17805

Introduction: KNM-BG 17805 is an approximately 4 cm long right partial calcaneus that lacks the proximal part of the heel process and the *sustentaculum tali* (Fig. 19). The distal articular surface and the peroneal tubercle are eroded away, and there is erosion along the lateral side of the facet for the proximal talocalcaneal joint. For the average of three measurements KNM-BG 17805 is similar in size to male *Papio* calcanei (Fig. 20; Table 8, Size).

Description and functional features: The distal part of the heel process is moderately mediolaterally compressed and bears a narrow dorsal ridge, as in many extant non-hominoids (Fig. 21, a). The medial part of the plantar surface of the process curves strongly plantarwards towards the broken proximal surface (Fig. 21, b). This region is almost certainly the most distal part of an expanded medial process of the heel tuberosity. Among extant anthropoids this tuberosity is well developed in a number of arboreal taxa. It indicates that the intrinsic toe flexors are well developed and can act independent of the long flexor muscles (Sarmiento, 1983). This function is important during various orthograde arboreal activities, such as climbing and clambering, that require toe-grasping by the dorsiflexed foot.

The preserved part of the specimen is not as proximodistally short as it is in extant hominoids (Table 8, Index 1). The whole bone is relatively shallow dorsoplantarly (Table 8, Index 2 and Index 3), particularly in the troughed region just distal to the facet for the proximal talocalcaneal joint (Fig. 21, c; Table 8, Index 4). The latter

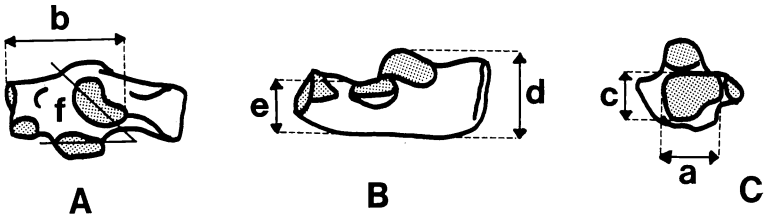

Figure 20. *Colobus polykomos* right calcaneus in dorsal (A), medial (B), and proximal (C) views, showing measurements taken (see also Table 8).

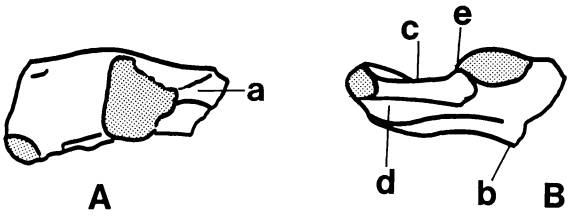

Figure 21. Morphological features of KNM-BG 17805 mentioned in the text. A, dorsal and B, medial views.

feature may indicate a particularly stable talocalcaneal configuration in full dorsiflexion. On the medial side of the body there is a well developed groove for the tendon of *m. flexor hallucis longus* (Fig. 21, d). The plantar lip of this groove is prominent and commences quite far proximally. The long, relatively deep groove is likely to channel a relatively well developed tendon, indicative of a well developed hallucial grasping function. The distal part of the facet for the proximal talocalcaneal joint is fairly steep in lateral view (Fig. 21, e). In dorsal view it is set at a slightly greater angle than in most anthropoids, but not to the degree seen in *Pan* (Table 8, Proximal facet angle).

Comparisons with other catarrhine fossil calcanei: Compared to the calcaneus of *Pliopithecus, Dendropithecus,* and *Limnopithecus* KNM-BG 17805 is mediolaterally broader distally (Table 8, Index 2), has a more pronounced groove for the tendon of *m. flexor hallucis longus*, and has a facet for the proximal talocalcaneal joint that faces dorsally rather than dorsomedially. However, KNM-BG 17805 and the calcanei of *Pliopithecus* and *Dendropithecus* (especially KNM-RU 1659) are otherwise similar, especially in the region of the medial process of the heel tuberosity. KNM-BG 17805 is dorsoplantarly shallower (Table 8, Index 3) than the calcanei of *Proconsul nyanzae, P. major,* and *Sivapithecus* (Harrison, 1982; Langdon, 1986; Rose, 1986). However, it is more similar, in this and other features, to *P. heseloni* (Rose, 1983), suggesting that some of these proportional features may be size-related.

Right distal first metatarsal, KNM-BG 17814

Introduction: KNM-BG 17814 consists of the distal 3.1 cm of a mildly weathered right first metatarsal (Fig. 22). There is some erosion to the proximal part of the

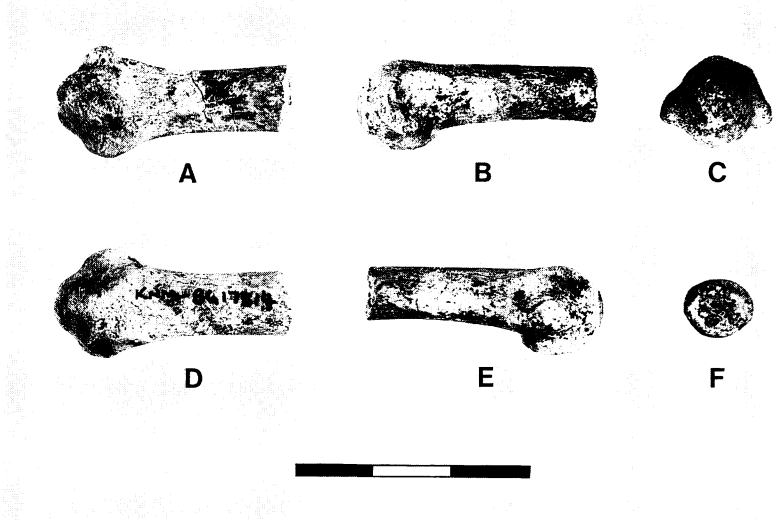

Figure 22. KNM-BG 17814 right first metatarsal. A, plantar; B, medial; C, distal; D, dorsal; and E, lateral views. F is the proximal cross section, with dorsal towards the top of the page. Scale in cm.

Table 9. First metatarsal indices and size comparisons

	Index 1 Distal shaft proportions a×100/b[1]	Index 2 Mediolateral shaft/head proportions b×100/c	Index 3 Head proportions d×100/c	Index 4 Mediolateral articular/head proportions e×100/c	Index 5 Articular proportions e×100/d	Index 6 Lateral sesamoid facet projection f×100/g	Index 7 Lateral facet proportions g×100/h	Size (a+b+d)/3
Pan troglodytes[2]	79.0[3]	74.9	95.2	60.0	63.1	79.6	24.9	11.7
	70-90	62-89	90-103	55-69	54-72	63-90	18-35	10.9-12.7
	7.2	8.7	4.1	4.3	4.9	9.6	5.8	
Hylobates spp.	73.2	71.9	86.9	53.8	62.1	74.6	39.6	5.8
	67-79	67-77	80-104	48-64	52-69	55-89	26-54	5.4-6.3
	4.0	3.9	7.5	5.0	5.1	10.9	9.2	
Papio cynocephalus	—	—	—	—	—	—	—	8.6
Male								8.2-9.4
Cercopithecus mitis	79.1	66.2	94.5	55.0	58.0	86.6	36.7	4.4
	70-84	59-80	89-105	50-63	51-67	72-99	33-42	3.5-5.5
	4.5	5.6	5.9	3.9	5.5	8.5	3.4	
Colobus polykomos	82.5	64.4	98.3	47.7	48.7	90.9	31.9	5.1
	75-88	61-72	89-107	42-54	39-59	72-108	26-36	4.7-5.6
	3.8	2.8	6.9	5.0	5.9	12.5	3.9	
Ateles spp.	80.8	70.7	99.9	65.4	65.7	83.2	25.9	5.5
	69-88	60-81	91-109	54-73	55-76	72-97	16-36	5.0-6.4
	5.7	6.9	5.2	5.9	5.7	7.5	7.0	
Cebus spp.	81.9	64.7	92.5	58.0	63.1	81.7	31.1	4.5
	76-93	57-73	85-102	53-67	53-76	62-103	24-35	4.0-5.1
	4.8	5.8	4.5	13.0	4.2	13.0	5.4	
Kenyapithecus sp. KNM-BG 17814	85.2	58.8	84.2	61.8	72.9	66.0	39.0	9.0
Pliopithecus vindobonensis Individual 1	90.9	65.3	101.3	62.0	61.2	85.2	28.5	7.1
Proconsul heseloni								
KNM-RU 2036AE	82.4	71.1	100.7	52.6	52.3	78.0	34.2	6.6
KNM-RU 2036BJ	81.7	63.0	89.6	58.0	64.8	88.9	29.2	6.7
KNM-RU 15074B	73.0	65.5	86.7	57.5	66.3	96.4	35.2	7.5
Proconsul nyanzae								
KNM-RU 5872E	76.8	69.0	89.5	58.0	64.8	64.2	28.8	10.5
KNM-MW 17392	84.2	66.0	95.8	53.6	56.0	90.0	26.9	10.4
Sivapithecus parvada GSP 14046	77.1	62.2	90.8	69.9	77.0	60.0	36.5	10.8

[1] These are the measurements illustrated in Figure 23.

[2] $n=10$ for combined sex samples, $n=5$ for the single sex sample.

[3] Mean, range and S.D.

lateral sesamoid facet. For the average of three dimensions it is similar in size to large male *Papio* first metatarsals (Fig. 23; Table 9, Size).

Description and functional features: The distal shaft is compressed dorsoplantarly to a greater extent than in most extant anthropoid first metatarsals, although it overlaps with the upper part of the range of several taxa (Table 9, Index 1). The shaft swells mediolaterally, and to a lesser extent dorsoplantarly, as it approaches the head. Compared to the distal shaft width the head is mediolaterally expanded to a greater extent that in almost all the specimens in the comparative sample (Table 9, Index 2). This expansion is also evident from the overall proportions of the head itself (Table 9, Index 3). The central articular surface of the head, for articulation with the proximal phalanx, is evenly curved in side view and in dorsal or plantar view (Fig. 24, a). It is ovoid in distal view, tapering more dorsally than plantarly (Fig. 24, b). Its mediolaterally broadest part is not markedly expanded compared to the total width of the head (Table 9, Index 4), but is markedly wide compared to its dorsoplantar dimension (Table 9, Index 5). On each side of the main facet there are relatively pronounced articular gutters for accommodation of the sesamoid bones of the metatarsophalangeal joint (Fig. 24, c). This is particularly marked on the lateral side, where the flange bearing the articular surface markedly projects laterally (Fig. 24, d; Table 9, Indices 6 and 7). Dorsally, the pits for the collateral ligaments are separated by a relatively narrow strip of the dorsal shaft surface, although this strip is not as narrow as it is on the metacarpal heads (Fig. 24, e).

In the overall morphology of its head, KNM-BG 17814 differs from all extant anthropoids, although it shares some features in common with, especially, *Cebus* and *Hylobates*. The mediolateral expansion of the head as a whole, and of the articular surfaces for the proximal phalanx in particular, suggest that abduction-adduction, and possibly axial rotatory movements are as important as flexion-extension movements in the functioning of the hallux. While the lateral sesamoid area is emphasized on all anthropoid first metatarsals, indicating an asymmetry of function in the glenoid plate and sesamoid complex, this asymmetry is particularly marked in KNM-BG 17814. As with the metacarpals, the relatively dorsal placement of the attachment sites of the collateral ligaments may allow appreciable abduction-adduction and axial rotatory movements without compromising the collateral ligaments' ability to

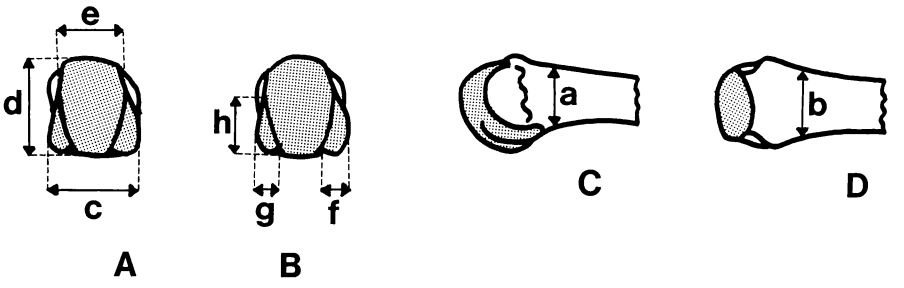

Figure 23. *Colobus polykomos* right first metatarsal in distal (A and B), medial (C), and dorsal (D) views, showing measurements taken (see also Table 9).

Table 10. Hallucial proximal phalanx indices and size comparisons

	Index 1 Distal shaft proportions a×100/b[1]	Index 2 Trochlear depth/width proportions c×100/d	Index 3 Trochlear length/width proportions e×100/d	Size (a+b+c+d+e)/5
Pan troglodytes[2]	66.7[3]	76.8	72.7	8.7
	63-73	69-87	67-79	7.9-9.8
	3.6	5.8	3.7	
Hylobates spp.	52.8	63.8	65.7	4.5
	44-60	57-69	60-74	4.2-5.5
	5.0	3.5	4.3	
Papio cynocephalus	—	—	—	5.5
Male				4.6-6.2
Cercopithecus mitis	64.1	66.9	69.1	3.6
	55-75	61-78	53-81	3.0-4.2
	5.8	5.2	7.9	
Colobus polykomos	70.1	64.8	70.1	4.0
	54-81	50-74	54-81	3.2-4.8
	8.2	6.6	8.2	
Ateles spp.	66.8	75.8	80.5	4.2
	59-75	66-85	70-93	3.9-4.6
	5.7	6.0	6.3	
Cebus spp.	63.7	64.1	70.1	3.6
	57-75	58-78	54-81	3.1-4.1
	5.2	7.0	8.2	
Kenyapithecus sp. KNM-BG 17813	71.3	70.4	67.3	7.1
Pliopithecus vindobonensis Individual 2	72.7	71.6	65.5	5.9
Proconsul heseloni				
KNM-RU 2036AF	53.5	62.6	64.2	5.3
KNM-RU 15074	63.5	65.8	70.8	5.9
Sivapithecus parvada GSP 14046	47.6	62.1	66.1	9.7

[1] These are the measurements illustrated in Figure 26.

[2] $n=10$ for combined sex samples, $n=5$ for the single sex sample.

[3] Mean, range and S.D.

stabilize the metatarsophalangeal joint in flexion. These functional complexes would seem to underlie an appreciable mobility of the first metatarsophalangeal joint. This in turn is most likely to be associated with a sophistication of the grasping function of the hallux, most likely exercised during arboreal activities.

Comparisons with other catarrhine fossil first metatarsals: Compared to the first metatarsals of *Pliopithecus* and *Proconsul*, KNM-BG 17814 has a more mediolaterally expanded head (Zapfe, 1960; Langdon, 1986). This expansion involves both the main facet, for articulation with the base of the proximal phalanx, and the lateral flange that articulates with the lateral sesamoid (Table 9, Indices 2, 3, 5, and 6). However, despite these proportional features all of these specimens share a strong guttering for the passage of the sesamoids as they move with the proximal phalanx during flexion-extension movements. By contrast, these gutters are minimally developed in *Sivapithecus* (Pilbeam *et al.*, 1980), where the head as a whole is less expanded than in KNM-BG 17814, but the main facet of the head contributes to most of its width (Table 9, Indices 2 and 4). This implies that in *Sivapithecus* movements other than flexion-extension may be even more important in the functioning of the metatarsophalangeal joint than in the KNM-BG 17814 individual.

Hallucial proximal phalanx KNM-BG 17813

Introduction: KNM-BG 17813 is an approximately 1.3 cm long uneroded fragment that preserves the most distal part of the shaft and the distal articular surface (Fig. 25). For the average of five measurements the specimen is intermediate in size between the largest male *Papio* and the smallest *Pan* specimens in the comparative sample (Fig. 26A and Table 10, Size).

Description, functional features, and comparisons with other catarrhine fossil hallucial proximal phalanges: The distal shaft is quite deep dorsoplantarly (Table 10, Index 1). This seems mostly due to an inflation of the plantar surface, present on the

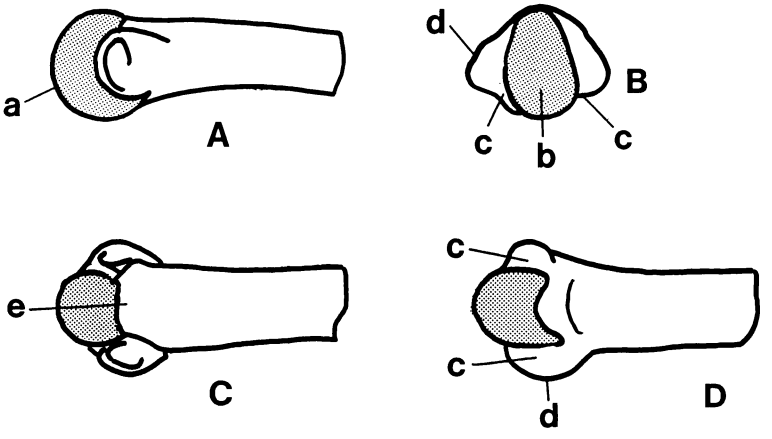

Figure 24. Morphological features of KNM-BG 17814 mentioned in the text. A, medial; B, distal; C, dorsal; and D, plantar views.

most proximal part of the specimen, which tapers as the plantar surface approaches the region of the head (Fig. 25C). The trochlea articular surface is quite deep dorsoplantarly, and moderately long proximodistally, although not to the extent seen in *Pan* or *Ateles* (Table 10, Indices 2 and 3). Overall, KNM-BG 17813 is quite similar to the hallucial proximal phalanges of predominantly quadrupedal anthropoids. The preserved parts are quite similar to the hallucial proximal phalanges of *Pliopithecus* (Zapfe, 1960) and *Proconsul* (Langdon, 1986). The shaft and trochlea of the *Sivapithecus* (Pilbeam *et al.*, 1980) hallucial proximal phalanx are dorsoplantarly shallower than in KNM-BG 17813.

Proximal phalanges KNM-BG 15531, 17774, and 17811.

Introduction: KNM-BG 15531 is a 1.1 cm long distal fragment that preserves the most distal part of the shaft and the trochlea, which is plastically deformed. Because of this deformation, this specimen is not considered in the descriptive section. KNM-BG 1774 is a 1.6 cm long fragment preserving the same parts as KNM-BG 15531, but without deformation. KNM-BG 17811 is 3.2 cm long and is only lacks the head (Fig. 25). The shaft is curved in dorsal or ventral view, as the result of a combination of fracture and plastic deformation. On the basis of the asymmetry of the basal tubercles, it is most likely from the right side.

Descriptions and functional features: The base of KNM-BG 17811 is mediolaterally broad, to the extent found only in the phalanges of *Cercopithecus* and *Cebus* among the comparative sample (Fig. 26B; Table 11, Indices 1 and 2). The articular surface for the metapodial head is oval and, as with the base as a whole, is mediolaterally broad (Table 11, Index 3). The surface faces proximodorsally, to the extent found in predominantly quadrupedal non-hominoid anthropoids (Table 11, Angle). In dorsal view the dorsal part of the surface is concave, as in non-hominoid phalanges. On the ventral aspect of the base there are well developed tubercles associated with the glenoid plate/sesamoid complex (Table 11, Index 4). The medial tubercle is more inflated than the lateral tubercle, and extends slightly further distally on the ventral surface of the shaft. The shaft has a flat ventral surface so that it is roughly semicircular in cross-section. The well developed ridges for the attachment of the flexor sheath are proximodistally short (Table 11, Index 5) and fairly distally situated on the shaft.

The shaft is mediolaterally broad in the region of the flexor sheath ridges, to an extent found in only occasional phalanges of extant anthropoids (Table 11, Index 6). As with the base and midshaft of KNM-BG 17811, the trochlea of KNM-BG 17774 is mediolaterally broad, to the extent found in some cercopithecids and *Cebus* (Table 11, Index 7). The degree of mediolateral expansion the proximal phalanx is similar to that already described for the metacarpal heads and for the first metatarsal. It implies the importance of abduction-adduction movements at the metapodial-phalangeal joint, possibly associated with arboreal activities such as climbing.

Comparisons with other catarrhine fossil proximal phalanges: KNM-BG 17811 differs from all comparable fossil phalanges in having a mediolaterally broader base and proximal articular surface (Table 11, Indices 1, 2, 3, and 4). KNM-BG 17811 and 17774 have a dorsoventrally shallower shaft and trochlea than the phalanges of *Pliopithecus* (Zapfe, 1960; Begun, 1988) and *Dryopithecus* (Begun, 1993). *Sivapithe-*

Table 11. Proximal phalangeal indices and angle

	Index 1 Base proportions a×100/b[1]	Index 2 Mediolateral shaft/base proportions c×100/b	Index 3 Proximal articular proportions d×100/e	Index 4 Articular/ base depth d×100/a	Index 5 Flexor ridge proportions f×100/g	Index 6 Midshaft proportions h×100/f	Index 7 Trochlear proportions i×100/j	Angle k
Pan troglodytes[2]								
Manual	96.1[3]	78.0	90.7	85.0	69.1	74.8	84.9	98.2
	87-109	69-87	79-103	81-90	61-75	65-98	80-91	90-105
	6.3	5.7	7.4	3.4	4.4	10.8	3.6	4.7
Pedal	98.8	68.6	95.4	86.6	66.9	90.8	82.4	96.0
	88-108	63-80	85-112	82-96	55-78	77-110	75-88	87-104
	5.7	4.8	8.6	4.3	7.1	11.8	4.5	5.0
Hylobates spp.								
Manual	93.4	80.7	91.4	89.1	54.2	66.6	95.1	99.7
	86-97	71-86	87-96	80-95	43-64	60-74	89-102	93-105
	3.5	4.7	3.2	5.0	7.2	5.1	4.8	3.7
Pedal	93.3	69.2	94.5	92.6	53.0	70.6	91.3	88.6
	82-108	62-81	89-103	87-96	40-62	62-85	77-102	84-93
	9.2	5.7	4.7	3.5	7.0	7.0	7.1	3.1
Cercopithecus mitis								
Manual	72.5	63.9	75.4	86.0	59.4	72.5	82.8	75.9
	64-82	50-74	64-85	76-99	54-66	59-86	73-99	72-80
	5.5	7.7	6.0	7.3	4.9	9.8	10.0	2.3
Pedal	75.8	59.4	74.9	87.6	50.5	73.4	75.7	72.9
	68-81	53-64	67-82	76-96	38-64	65-89	70-83	70-80
	4.2	4.1	5.0	6.0	7.8	7.2	4.2	3.3
Colobus polykomos								
Manual	79.3	69.1	82.4	85.4	44.5	67.7	77.9	77.0
	76-85	61-85	73-95	75-96	37-53	64-71	71-83	73-85
	2.9	7.1	7.2	7.1	4.8	2.3	4.4	4.5
Pedal	78.3	66.7	83.1	84.6	41.8	70.2	78.2	76.0
	75-83	59-76	77-97	78-94	34-50	66-81	70-84	69-82
	2.5	6.3	6.3	5.2	4.5	4.5	5.3	4.3
Ateles spp.								
Manual	88.4	72.4	90.6	87.5	35.5	69.5	86.0	87.7
	82-98	62-78	81-98	72-95	29-46	63-81	79-92	83-93
	5.1	4.9	4.5	6.7	5.5	5.1	3.9	3.5
Pedal	91.2	68.7	89.2	84.0	33.6	72.0	87.6	68.3
	80-104	60-81	79-97	78-91	30-38	63-82	80-92	65-75
	7.0	6.0	5.3	5.0	2.8	6.8	4.5	3.4
Cebus spp.								
Manual	75.6	60.0	73.1	85.4	47.6	71.3	75.9	73.8
	69-84	54-67	67-83	76-96	37-59	63-83	70-83	65-80
	4.8	4.7	5.4	5.7	7.5	7.5	3.8	4.6
Pedal	77.5	59.4	79.8	88.7	50.5	75.8	77.0	71.0
	71-81	52-67	74-84	84-94	40-57	66-82	74-90	60-81
	3.4	5.0	3.3	4.0	5.1	5.1	5.3	5.7
Kenyapithecus sp.								
KNM-BG 17774	—	—	—	—	—	—	71.8	—
KNM-BG 17811	73.1	55.2	71.8	80.7	64.5	61.1	—	65
Aegyptopithecus zeuxis								
DPC 1005	66.7	70.6	62.5	88.3	77.6	53.2	70.7	65
DPC 7107	78.1	60.2	92.5	79.0	72.5	68.3	69.3	61
Pliopithecus vindobonensis								
Individuals 2 and 3	85.9	61.9	88.2	76.1	32.2	87.5	85.8	—
n=8, 9, or 10	79-94	55-69	76-102	63-82	26.6	79-95	73-106	
	6.1	4.9	10.6	5.7	4.9	5.6	11.8	
Proconsul heseloni	78.7	68.0	81.5	80.5	70.6	64.6	78.7	70.5
KNM-RU 2036S, T,	67-88	64-76	72-89	70-90	54-91	51-78	73-86	61-77
V, AA, AF, BK,	6.6	4.7	6.2	7.1	10.8	6.3	4.1	5.8
BQ, BR, BY, BZ								
KNM-RU 15074A,								
KNM KPS individuals								
1, 3, and 8.								
n=5, 8, 9, 16, or 18								
Proconsul nyanzae	—	—	—	69.7	62.0	57.5	70.0	—
KNM-RU 5872R, 14190,					57-65	54-62	67-73	
15100H & O, 18383					3.8	3.1	3.5	
n=1, 2, or 4								
Dryopithecus brancoi	—	—	—	—	—	73.3	85.2	—
RUD 78								
Sivapithecus parvada	89.8	72.5	80.2	75.5	66.3	56.4	75.4	79
GSP 17154, 19700,					60-72	54-60	71-78	
19833					8.5	3.4	3.9	
n=1, 2, or 3.								

[1] These are the measurements illustrated in Figure 26.
[2] n=10.
[3] Mean, range and S.D.

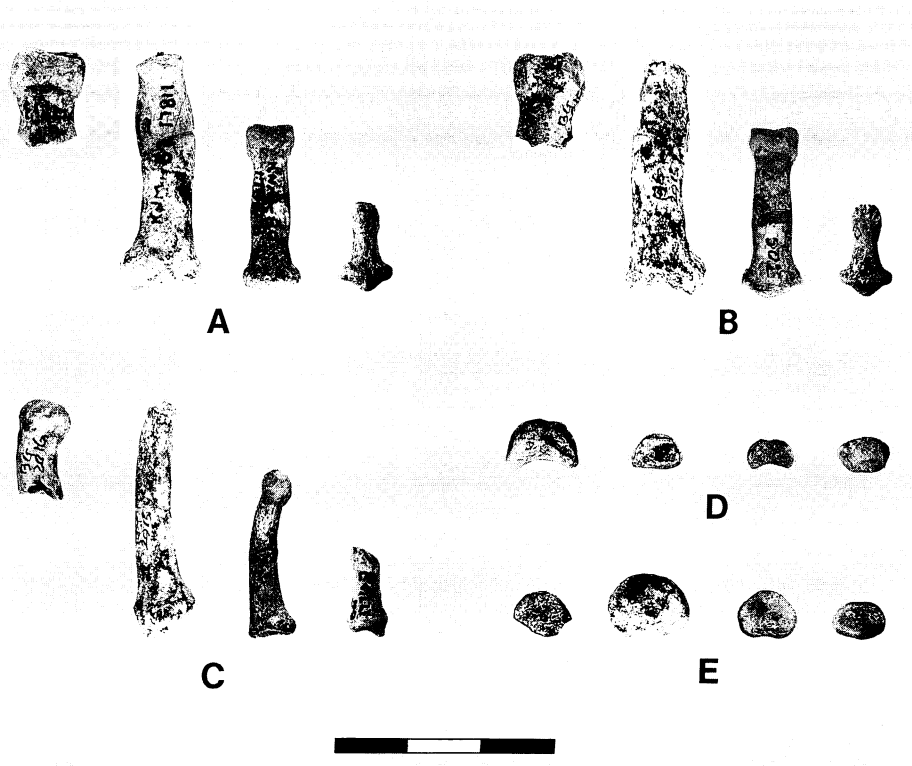

Figure 25. From left to right in each set, KNM-BG 17813 hallucial proximal phalanx, KNM-BG 17811 proximal phalanx, KNM-BG 17808 middle phalanx, and KNM-BG 17748 terminal phalanx. A, ventral; B, dorsal; C, right side; D, distal; and E, proximal views. The distal cross section of KNM-BG 17811 is shown in D, and the proximal cross section of KNM-BG 17813 is shown in E. Scale in cm.

cus phalanges (Rose, 1986) are shallower at midshaft and have a more proximally facing proximal articular surface. Apart from the differences in the morphology of the base, the *Kenyapithecus* specimens are otherwise similar to those of *Proconsul* (Begun *et al.*, 1994).

Middle phalanges KNM-BG 15540, 17808, and 17812.

Introduction: KNM-BG 15540 is a 1.1 cm long proximal fragment, preserving the base and the proximal part of the shaft. KNM-BG 17808 is an almost complete specimen, 2.3 cm in length (Fig. 25). The proximal articular surface is eroded except for its most ventral part. KNM-BG 17812 is 1.3 cm long and represents approximately the distal half of the bone. The following description concentrates on KNM-BG 17808, while details of the morphology of the base are taken from KNM-BG 15540.

Description and functional features: The complete phalanx is relatively short, to the extent found in some *Cercopithecus* and *Pan* middle phalanges (Fig. 26C; Table 12, Indices 1, 2, and 3). The base is oval in proximal view. It it is dorsoventrally deeper than is usual in *Cercopithecus* middle phalanges, but shallower than is usual in those of *Hylobates* (Table 12, Index 4). As is usual in extant anthropoids other than large hominoids, the proximal articular surface consists of two concave surfaces separated by a dorsoventral midline ridge. In dorsal view these surfaces are set at a slight angle to each other, so that the midline ridge represents the most proximally situated part of the articular surface as a whole. This morphology mirrors the relatively deeply grooved articular surface of the trochlea of the proximal phalanx. Dorsally and ventrally, the midline ridge expands into modestly developed lips. The shaft is dorsoventrally moderately compressed at mid-shaft (Table 12, Index 5). The ventral surface of the shaft is convex about the midline, and is flanked by well developed ridges for the attachment of the flexor sheath. The trochlea is quite mediolaterally broad, but within the upper part of the ranges of most of the comparative samples (Table 12, Index 6). It is correspondingly dorsoventrally shallow, to the extent found in most *Cercopithecus* middle phalanges (Table 12, Index 7). The trochlea is grooved to the extent found in extant anthropoids other than large hominoids. In their overall morphology the *Kenyapithecus* middle phalanges are most similar to those of cercopithecids, reflecting the participation of the middle phalanges in the type of cheirideal placement and grasping associated with quadrupedal activities.

Comparisons with other catarrhine fossil middle phalanges: Specimens similar to the Nachola specimens have been described for *Kenyapithecus africanus* from Maboko (McCrossin, 1994a, 1994b; McCrossin and Benefit 1994, 1995). The Nachola *Kenyapithecus* specimens are similar to those of *Proconsul* (Begun *et al.*, 1994). KNM-BG 17808 is less elongated (Table 12, Indices 1, 2, and 3) than the middle phalanges of *Pliopithecus* (Zapfe, 1960). Also, the base and trochlea are dorsoventrally shallower than those of most of the *Pliopithecus* specimens (Table 12, Indices 4 and 7). By contrast, compared to *Simiolus* (Rose *et al.*, 1992), the *Kenyapithecus* specimens are dorsoventrally deep (Table 12, Indices 4 and 5). Compared to *Dryopithecus* specimens (Begun, 1993), KNM-BG 17808 is relatively longer (Table 12, Indices 1 and 3).

Table 12. Middle phalangeal indices

	Index 1 Base width/ total length a×100/b[1]	Index 2 Midshaft width/ total length c×100/b	Index 3 Trochlear width/total length d×100/b	Index 4 Base proportions e×100/a	Index 5 Midshaft proportions f×100/c	Index 6 Trochlear/ base width d×100/a	Index 7 Trochlear proportions g×100/d
Pan troglodytes[2]							
Manual	37.9[3]	23.9	25.0	82.1	65.2	65.8	72.1
	34-42	20-28	22-32	73-89	58-70	58-79	68-77
	2.5	2.0	3.6	6.0	4.1	6.1	2.6
Pedal	42.0	26.1	32.0	89.5	77.7	76.2	71.3
	37-48	22-33	26-38	80-97	66-82	64-85	64-79
	3.7	3.4	4.2	5.6	4.6	6.7	5.6
Hylobates spp.							
Manual	23.5	17.4	17.1	89.6	60.0	73.1	73.1
	20-26	15-19	15-19	83-100	54-65	65-86	69-78
	2.5	1.5	1.7	5.3	3.8	5.6	2.9
Pedal	29.3	20.3	23.8	90.9	61.8	81.2	67.3
	24-32	18-24	18-26	82-99	53-67	69-89	60-74
	2.4	1.7	2.6	5.0	4.9	8.0	4.9
Cercopithecus mitis							
Manual	35.4	23.5	27.5	71.2	66.7	77.8	63.4
	31-39	22-27	23-30	62-79	61-75	67-89	58-70
	3.2	1.9	2.5	5.4	5.3	6.3	4.0
Pedal	36.0	23.0	27.3	73.3	67.5	75.9	62.5
	31-42	19-27	22-33	68-80	61-76	70-85	57-66
	4.2	2.6	3.7	3.7	4.8	4.9	2.8
Colobus polykomos							
Manual	31.8	21.9	24.4	78.4	62.0	76.7	65.7
	27-36	19-26	20-28	69-92	55-65	72-86	59-74
	2.4	2.4	2.6	6.6	2.9	5.3	4.8
Pedal	31.3	21.1	23.8	77.4	62.2	76.0	64.6
	27-35	19-23	20-27	69-87	58-65	66-82	57-70
	2.5	1.4	2.5	6.5	2.6	5.4	4.4
Ateles spp.							
Manual	27.2	19.3	20.6	82.1	61.0	75.6	68.5
	23-30	17-22	18-23	74-93	56-67	72-80	62-76
	2.2	1.8	1.6	5.4	3.4	3.0	5.5
Pedal	28.8	20.1	22.6	88.1	59.0	78.6	69.3
	26-33	18-23	19-26	75-97	53-66	68-85	63-80
	2.5	1.7	2.3	6.1	4.4	5.3	6.1
Cebus spp.							
Manual	32.8	20.9	25.6	78.4	73.1	78.3	64.9
	30-36	18-25	23-28	74-84	66-82	73-87	62-68
	2.5	2.5	1.7	3.6	4.6	4.8	1.9
Pedal	31.9	19.4	24.6	77.7	76.2	77.2	66.7
	28-35	18-22	22-28	69-86	73-80	71-82	62-71
	2.2	1.5	1.7	4.6	2.2	3.9	2.9
Kenyapithecus sp.							
KNM-BG 15540	—	—	—	78.8	—	—	—
KNM-BG 17808	35.3	26.1	29.0	79.7	65.7	82.2	63.7
KNM-BG 17812	—	—	—	—	67.3	—	66.8
Pliopithecus	30.2	23.2	24.3	88.1	70.0	80.7	70.3
vindobonensis	25-34	20-26	21-29	77-93	63-76	69-88	61-85
Individuals	3.3	1.9	3.2	4.8	4.4	6.7	6.9
2 and 3							
$n=10$							
Simiolus enjiessi	—	—	—	71.5	50.4	—	—
KNM-WK 17171E							
Proconsul heseloni	33.3	26.2	28.5	84.8	59.9	85.9	59.3
KNM-RU 2036U, X,	29-39	22-34	25-33	62-103	51-74	80-93	55-71
Y, Z, BV, CA,	3.4	3.2	2.8	8.9	5.6	4.0	4.1
CB, CC, CX, DK							
KNM KPS individuals							
1, 2, 3, 5, 8 and 9							
$n=13$, 14, 16, 20, or 21							
Proconsul nyanzae	34.5	26.7	28.7	81.3	61.3	83.6	61.2
KNM-RU 5872S,	29-38	20-33	25-33	74-85	56-67	73-89	59-64
15100I & J, &	5.2	5.0	3.1	6.0	4.7	8.8	2.0
SO 974							
$n=3$ or 4							
Dryopithecus brancoi							
RUD 81	38.0	22.4	30.4	74.4	75.5	80.00	72.2
RUD 95	—	34.5	37.6	—	60.3	—	62.2

[1] These are the measurements illustrated in Figure 26.
[2] $n=10$.
[3] Mean, range and S.D.

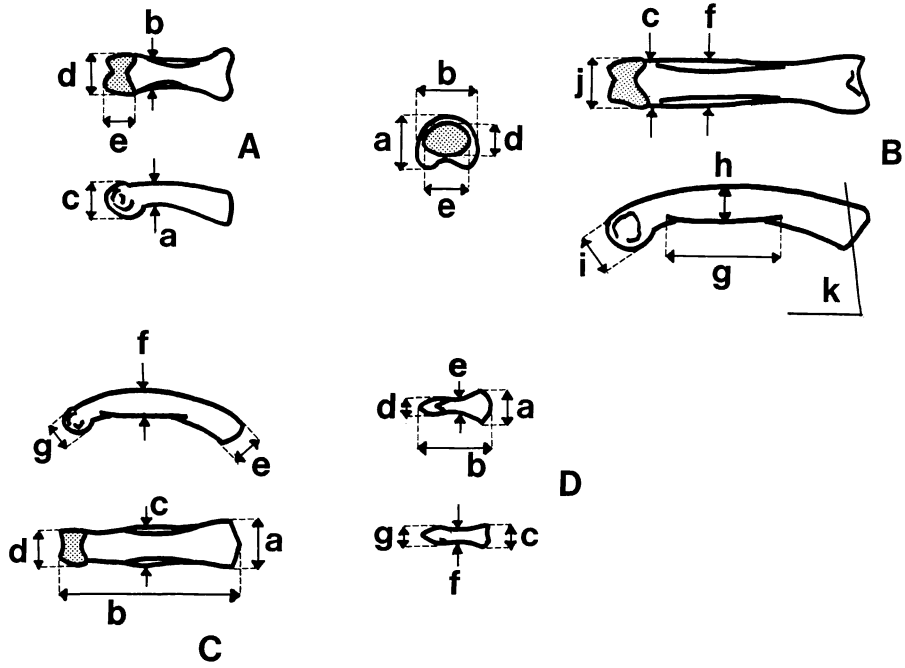

Figure 26. *Colobus polykomos* hallucial phalanx (A), non-hallucial pedal proximal phalanx (B), pedal middle phalanx (C), and non-hallucial pedal terminal phalanx (D) from the left foot, showing measurements taken. A illustrates plantar (above) and lateral (below) views. B illustrates proximal (left), plantar (above right), and lateral (below right) views. C illustrates lateral (above) and plantar (below) views. D illustrates dorsal (above) and lateral (below) views. See also Tables 10, 11, 12, and 13.

Terminal phalanges KNM-BG 17748 and 17818.

Introduction: KNM-BG 17748 is 11.5 mm long and KNM-BG 17818 is 9.2 mm long. They are both complete and uneroded (Fig. 25). They are similar in their proportional and other morphological features. KNM-BG 17818 fits perfectly with the middle phalanx KNM-BG 17808, which is from the same site, BGI. KNM-BG 17748 fits quite well with the middle phalanx KNM-BG 17812. These two specimens are also from the same site, BGX. It is therefore possible that each pair of specimens is associated. Whether or not this is so, the size match with the middle phalanges, together with morphological features, exclude the possibility that the terminal phalanges are from the hallux or pollex. However, in some proportional features the specimens are similar to the pollicial terminal phalanges of some extant anthropoids. Thus, although the fossil specimens are considered to be from digits other than the first, proportional features of pollicial terminal phalanges are included in Table 13. The following description applies equally to KNM-BG 17748 and KNM-BG 17818.

Description and functional features: The phalanx is proximodistally short compared to most of its other dimensions (Fig. 26D; Table 13, Indices 1, 2, 3, and 4).

The base is relatively broad, continuing the trend seen in the metapodials and the proximal and middle phalanges (Table 13, Index 5). The articular surface is slightly V-shaped in dorsal view, so as to fit with the trochlear shape of the middle phalangeal head. There is a pronounced ventral lip. The shaft is slightly dorsoventrally deeper than it is wide (Table 13, Index 6). It rapidly narrows as it passes distally from the base, and is at its narrowest just proximal to the ungual tuberosity. Compared to the width of the base, the shaft is narrower than in most of the comparative samples (Table 13, Index 7). The ungual tuberosity is unremarkable in its proportions (Table 13, Index 8). Its dorsal aspect bears a series of radiating ridges where it underlies the nail base. It apparently supported a quite broad nail. The *Kenyapithecus* specimens are not closely similar to those in any of the comparative samples. The relatively short shaft is quite similar to the condition in terrestrial cercopithecids such as *Papio*. However the mediolateral expansion of the base, as in other cheirideal elements, may indicate the importance of a secure grasping capability in the hands and/or feet.

Comparisons with other catarrhine fossil terminal phalanges: *Kenyapithecus* differ from most of the other fossils, as well as from most extant anthropoid terminal phalanges, in having a broad base, compared especially with total length and with the minimum width of the shaft (Table 13, Indices 1 and 7). The shaft is also quite deep dorsoventrally (Table 13, Index 6). However, there is overlap in most features with at least some *Proconsul* specimens, and in overall morphology the *Kenyapithecus* specimens are quite similar to, if somewhat more robust than the *Proconsul* (Begun *et al.*, 1994) and possible *Rangwapithecus* specimens. Terminal phalanges of *Kenyapithecus africanus* from Maboko are described as most resembling those of *Pliopithecus* and extant cercopithecoids (McCrossin, 1994b; McCrossin and Benefit, 1995).

Terminal thoracic vertebra KNM-BG 17826

Introduction: KNM-BG 17826 is an eroded centrum, approximately 2.3 cm long (Fig. 27). The pedicle and part of the lamina are preserved on the left side, but only the base of the pedicle is present on the right. The epiphyses are lacking on both the cranial and caudal face of the centrum, and there is additional erosion, especially ventrally, and especially on the cranial face. The presence of cranial facets for the articulation of ribs indicates that this is from the terminal thoracic region. The fact that the pedicles slope medially as they pass dorsally (as in lumbar vertebrae), and that the origin of the transverse process is from the caudoventral part of the pedicle strongly suggests that KNM-BG 17826 is a twelfth thoracic vertebra. It is thus compared with data from terminal thoracic vertebrae in Table 14. For the average of three measurements, KNM-BG 17826 is similar in size to male *Papio* terminal thoracic vertebrae (Fig. 28A and B; Table 14, Size).

Description and functional features: The centrum is craniocaudally elongated to the extent found in most extant anthropoid twelfth thoracic vertebrae (Fig. 28A and B; Table 14, Indices 1 and 2). The reniform cranial face is broader than it is deep, to the extent seen in most extant anthropoids in the comparative sample other than *Cercopithecus* (Table 14, Index 3). The centrum is asymmetrical about the midline, so that the midline keel is to the left of the midline (Fig. 29A, a). Ventrally, the cen-

Table 13. Terminal phalangeal indices

	Index 1 Base width/ total length a×100/b[1]	Index 2 Base depth/ total length c×100/b	Index 3 Ungual width/ total length d×100/b	Index 4 Shaft width/ total length e×100/b	Index 5 Base proportions c×100/a	Index 6 Shaft proportions f×100/e	Index 7 Shaft/base width e×100/a	Index 8 Ungual proportions g×100/d
Pan troglodytes								
Pollicial	48.8[2]	36.3	31.0	22.2	73.3	102.2	44.9	69.6
$n=10$	45-53	29-42	26-36	17-26	64-87	85-122	37-52	61-79
	2.8	5.0	2.9	3.0	7.3	12.5	5.8	6.6
Manual 2-5	48.0	39.8	27.9	21.3	79.4	108.9	43.7	75.8
$n=10$	42-51	32-54	26-30	16-27	72-87	95-130	34-51	66-85
	2.6	6.8	1.6	3.3	5.2	11.1	5.0	6.4
Pedal 2-5	54.4	47.2	32.3	25.9	85.3	114.9	48.5	80.8
$n=10$	44-66	37-66	26-40	20-32	80-92	105-127	46-51	64-95
	7.8	9.4	4.2	4.3	4.0	8.6	2.0	9.9
Hylobates spp.								
Pollicial	47.4	32.7	26.5	26.3	73.7	59.3	50.1	74.6
$n=4$	40-55	28-36	24-30	20-31	62-90	50-71	45-58	71-80
	6.6	3.6	2.5	4.6	12.0	9.4	5.8	4.3
Manual 2-5	41.2	33.9	20.7	23.5	72.9	102.4	52.0	97.8
$n=5$	38-47	28-48	17-24	15-30	68-77	78-129	41-64	82-112
	3.8	8.0	2.7	5.8	3.9	22.0	11.0	12.2
Pedal 2-5	45.7	35.7	21.7	21.0	76.6	111.2	46.3	91.9
$n=4$	37-52	31-40	18-26	17-25	74-79	100-124	38-53	84-97
	6.7	3.8	3.8	3.5	1.9	9.8	6.4	5.4
Cercopithecus mitis								
Pollicial	70.7	45.3	40.6	33.9	63.4	74.2	47.6	77.9
$n=7$	61-80	37-53	32-52	30-37	55-70	70-84	42-52	66-93
	6.0	4.7	7.2	2.4	5.0	5.6	4.2	11.6
Manual 2-5	55.9	41.7	26.7	26.7	79.2	105.2	51.3	101.3
$n=6$	51-61	38-44	22-33	24-31	71-92	86-124	41-70	78-137
	4.3	2.4	4.2	3.0	7.9	15.2	10.9	21.4
Pedal 2-5	50.2	37.4	24.3	24.6	75.8	108.9	50.6	113.8
$n=6$	45-57	34-41	18-30	21-29	73-78	92-134	43-56	92-135
	4.9	2.7	4.7	3.4	1.9	17.2	5.1	16.7
Colobus polykomos								
Pollicial[3]	74.5	64.1	64.6	67.9	82.6	83.4	91.4	76.8
$n=7$	58-91	47-80	44-86	50-84	73-92	77-89	80-109	65-94
	13.6	14.3	16.3	13.2	7.6	4.6	9.3	10.1
Manual 2-5	46.0	36.9	22.6	22.8	80.2	129.8	49.6	128.4
$n=10$	40-52	32-43	19-28	19-26	74-88	103-162	44-53	103-156
	3.8	3.5	2.9	2.6	4.3	17.7	3.0	18.8
Pedal 2-5	45.9	38.7	22.7	22.0	82.4	127.6	48.0	123.7
$n=10$	39-56	33-47	17-26	17-27	75-87	109-154	39-57	97-155
	4.9	4.1	3.1	3.2	4.3	15.2	5.0	21.3
Areles spp.								
Manual 2-5	43.5	32.9	23.3	22.1	75.7	95.7	51.0	83.9
$n=10$	36-50	28-35	16-33	20-24	68-80	83-110	48-55	60-105
	3.7	2.4	5.1	1.2	4.2	8.2	2.9	15.4
Pedal 2-5	42.8	32.1	23.5	21.1	75.4	107.1	49.8	101.1
$n=10$	34-48	28-35	18-31	18-24	70-83	87-126	44-60	75-123
	4.7	2.6	4.5	1.5	3.9	13.4	5.8	17.4
Cebus spp.								
Pollicial	42.0	26.1	23.3	20.4	61.2	88.2	48.6	80.5
$n=8$	36-46	22-29	18-28	17-22	58-64	70-100	42-57	68-96
	3.3	2.0	4.0	1.9	2.3	11.9	4.7	9.2
Manual 2-5	36.3	32.6	21.5	18.1	88.9	122.3	50.0	83.5
$n=10$	33-39	29-37	14-29	12-24	81-94	98-148	36-71	70-102
	2.1	2.2	4.5	4.1	4.5	16.5	11.0	10.5
Pedal 2-5	38.2	34.4	21.5	18.0	90.0	122.7	47.2	87.9
$n=9$	35-42	29-39	17-26	15-24	81-98	90-139	38-62	66-108
	2.4	3.1	3.1	3.0	5.8	17.7	7.6	15.1
Kenyapithecus sp.								
KNM-BG 17748	65.2	45.4	38.9	27.4	69.6	106.7	42.0	87.0
KNM-BG 17818	69.8	46.3	37.7	26.3	66.3	107.4	37.6	75.5
Pliopithecus vindobonensis	45.6	30.1	25.3	21.6	66.1	101.9	47.3	90.9
Individual 3, manual 2nd digit								
?Dendropithecus macinnesi not 1st digit								
KNM-CA 1850	49.5	33.0	39.2	35.4	66.6	81.6	71.7	77.9
KNM-CA 2131	51.4	32.1	35.1	31.4	62.6	85.9	61.1	71.7
?Rangwapithecus gordoni	59.0	40.1	36.6	34.2	67.8	90.7	57.4	81.2
not 1st digit	52-76	34-54	29-63	27-54	62-71	85-98	49-71	70-98
KNM-SO 976, 981, 982, 1375, LG 1479, CA 428, 563, 588, 629, 634, 1315 $n=11$	7.2	5.9	9.5	7.5	2.8	3.8	5.6	8.4
Proconsul heseloni pollicial								
KPS PH40	78.8	53.3	47.9	43.7	67.6	91.0	55.4	87.9
manual & pedal 2-5	55.2	38.5	34.7	31.9	71.3	95.5	58.1	84.5
KNM-RU 2036DL, DM,	37-77	32-49	25-52	21-44	53-93	72-117	40-79	65-100
KPS individuals 1 and 3 $n=10$ or 11	11.5	5.7	7.6	7.5	11.8	14.5	11.7	12.2
Proconsul nyanzae pollicial	64.5	40.7	39.6	30.6	63.2	92.9	47.9	69.6
KNM-RU 1766 & 15100B,LG 1480, $n=3$	55-70	34-48	36-43	30-32	57-70	82-106	44-54	62-74
	8.2	6.7	3.7	0.96	6.7	12.2	5.5	6.7
not 1st digit								
KNM-RU 15100L	74.4	42.6	41.9	34.9	57.3	95.6	56.3	81.5

[1] These are the measurements illustrated in Figure 26. [2] – Mean, range and S.D.
[3] *Colobus* pollicial terminal phalanges are highly variable in morphology. In *Areles*, the terminal phalanges are vestigial.

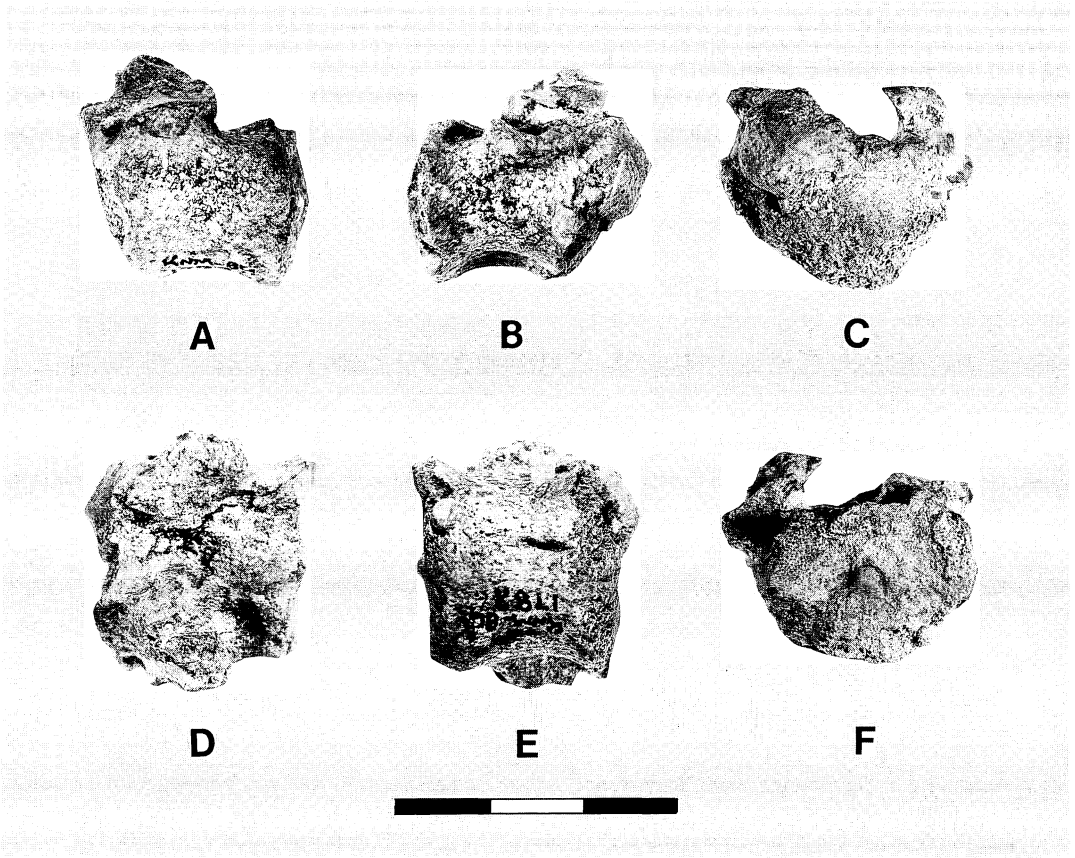

Figure 27. KNM-BG 17826 terminal thoracic vertebra. A, left; B, right; C, cranial; D, dorsal; E, ventral; and F, caudal views. Scale in cm.

trum is excavated on the right side, which most likely represents a pre-mortem and possibly pathological condition (Fig. 29A, b). A foramen for a communicating vein is present on this surface (Fig. 29B, c). A modest ventral keel is present, slightly to the left of the midline. Excavations at each craniodorsal corner of the centrum most likely represent regions for articulation with the heads of the ribs (Fig. 29B, d). Left and right attachment sites for slips of the posterior longitudinal ligament are present on the dorsocaudal edge of the centrum (Fig. 29C, e).

Only the root of the pedicle is present on the right (Fig. 29C, f), while most of the left pedicle is preserved (Fig. 29A, g). Compared with the length of the centrum, the pedicle is craniocaudally shorter than is usual in anthropoids other than *Pan* (Table 14, Index 4), but resembles extant anthropoids other than *Pan* in being moderately robust (Table 14, Index 5). The pedicle is quite short dorsoventrally, and its cranial margin inclines medially while its caudal margin inclines laterally. The root of the lamina is present craniomedially (Fig. 29A, h), while the root of the transverse process is present ventrocaudally on the lateral surface of the pedicle (Fig. 29A, i).

There are few obvious functional conclusions to be drawn from the morphology of KNM-BG 17826. It is generally similar to the vertebral centra of many extant non-hominoid anthropoids. In particular, it is relatively longer craniocaudally than in extant hominoids. However, the preserved morphology does not enable any distinc-

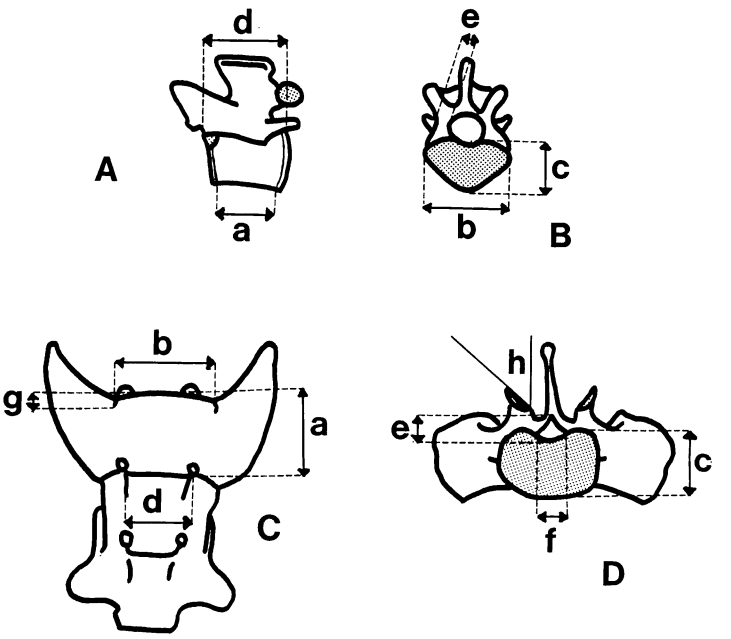

Figure 28. *Colobus polykomos* last thoracic vertebra in left (A) and cranial (B) views, and sacrum in ventral (C) and cranial (D) views, showing measurements taken (see also Tables 14 and 15).

tion to be made between, for example, the use of the vertebral column in predominantly suspensory or predominantly quadrupedal activities.

Comparisons with other catarrhine fossil lower thoracic vertebrae: KNM-BG 17826 is somewhat craniocaudally shorter and dorsoventrally deeper (Table 14, Indices 1 and 3) than the terminal thoracic vertebra of *Pliopithecus*. It is generally similar to the small ape terminal thoracic centrum, KNM-WS 12603 (Rose *et al.*, 1992), but has a more robust pedicle (Table 14, Index 5). It is most similar to the corresponding vertebra of *Proconsul nyanzae* (Ward, 1991, 1993).

Lumbar vertebra KNM-BG 15527

Introduction: KNM-BG 15527 is a 2.3 cm long weathered lumbar vertebral centrum (Fig. 30). Most of the ring epiphysis is present on the cranial face, but there is heavy erosion of the caudal face. Only the bases of the pedicles and transverse processes are preserved. Although the specimen is evidently not from a terminal lumbar vertebra, it cannot be placed within the rest of the lumbar sequence. For this reason it is compared with samples drawn from several mid-lumbar levels (Table 14), and size comparisons have not been attempted.

Description and functional features: The centrum is relatively longer cra-

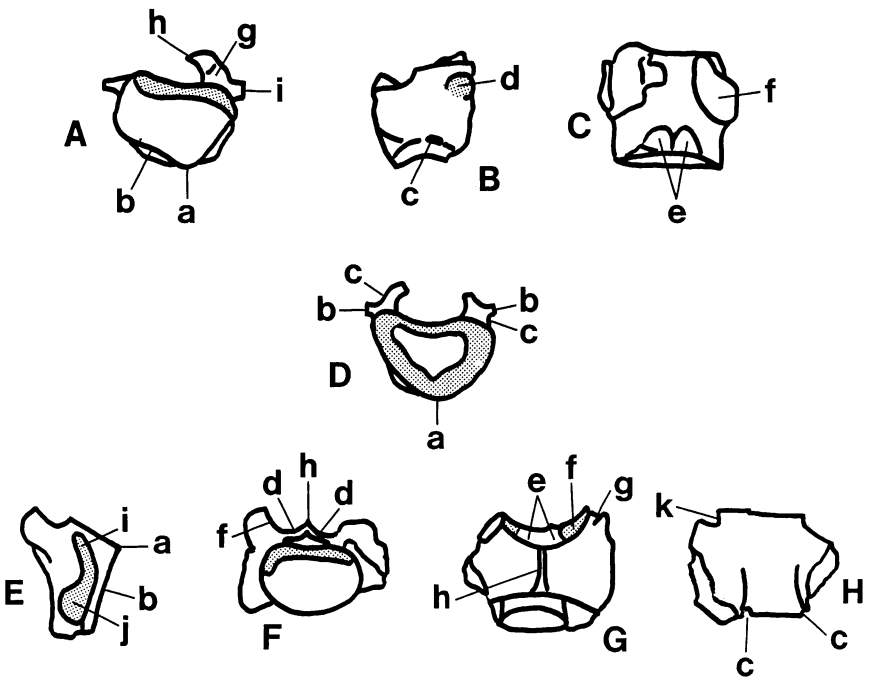

Figure 29. Morphological features mentioned in the text for KNM-BG 17826 in cranial (A), right (B), and dorsal (C) views; KNM-BG 15527 in cranial view (D); KNM-BG 17822 in right (E), cranial (F), dorsal (G), and ventral (H) views.

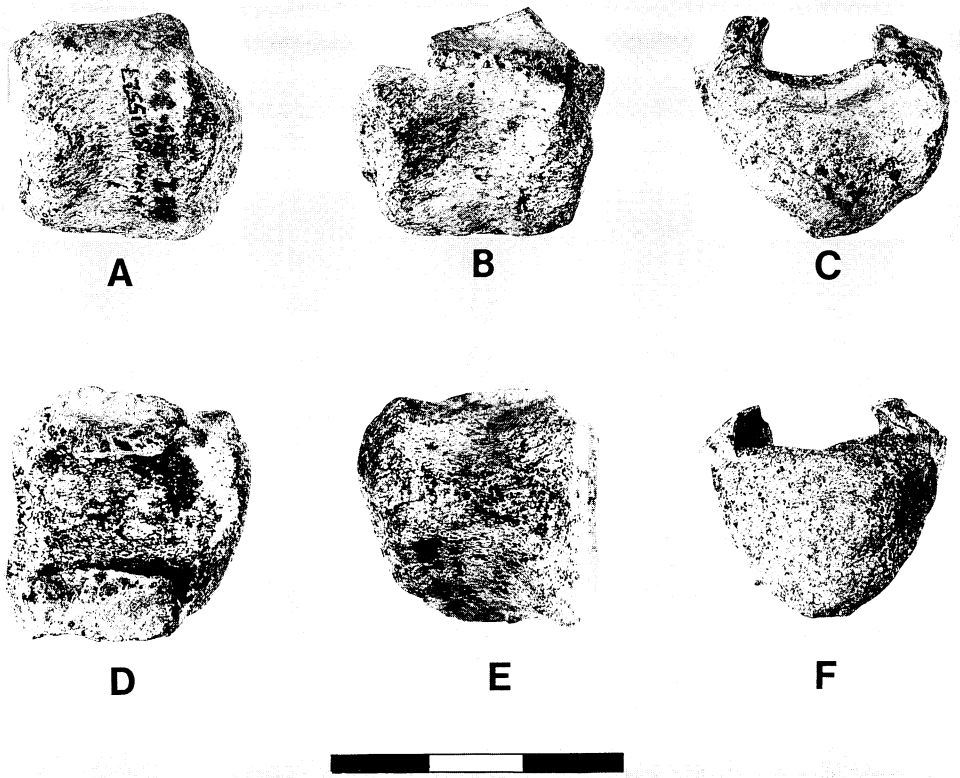

Figure 30. KNM-BG 15527 lumbar vertebra. A, left; B, right; C, cranial; D, dorsal; E, ventral; and F, caudal views. Scale in cm.

niocaudally than in extant hominoids and *Ateles*, and most similar in length to *Colobus* and *Cebus* mid-lumbar vertebrae (Fig. 28A and B; Table 14, Indices 1 and 2). However, the cranial face is relatively deep dorsoventrally, to the degree found in extant hominoids and *Ateles* (Table 14, Index 3). This is partly due to the presence of a well developed ventral median keel, which results in the cranial face being distinctly triangular in outline (Fig. 29D, a). The ring epiphysis on this face also is also triangular. The sides of the centrum are concave in ventral view. Despite the proportional similarities, KNM-BG 15527 is most similar to extant non-hominoids in these features. Pits (multiple on the right) for communicating veins are present on the sides of the centrum. The roots of the transverse processes are present dorsally on the centrum, adjacent to the bases of the pedicles (Fig. 29D, b and c). They occupy approximately half the craniocaudal length of the centrum. The pedicle bases are robust compared to those of cercopithecids, but gracile compared with those of other anthropoids except *Cebus* (Table 14, Index 5). As with KNM- BG 17826, it is not possible to reach specific conclusions concerning function in KNM-BG 15527. It is generally similar to non-hominoid lumbar vertebrae, particularly in its relative length, presence of a ventral keel, and the origin of the transverse processes from the centrum, rather than from the neural arch. These are features associated with predominantly pronograde extant anthropoids.

Comparisons with other catarrhine fossil lumbar vertebrae: KNM-BG 15527 is closely similar to *Proconsul heseloni* and *P. nyanzae* lumbar vertebrae (Ward, 1991, 1993) in most of its morphological and proportional features. It differs from the large hominoid vertebra UMP 67.27 in being more triangular in cranial view, in the site of origin of the transverse processes, in its relative length, and in having less robust pedicles. UMP 67.28 is more like extant hominoids in its morphology (Walker and Rose, 1968; Sanders and Bodenbender, 1994).

Sacral vertebra KNM-BG 17822

Introduction: KNM-BG 17822 is a first sacral vertebra, approximately 2.5 cm long craniocaudally and 3.1 cm wide (Fig. 31). Most of the centrum is complete except for ventral part of the ring epiphysis on the cranial face. Most of the neural arch structures are preserved, except for the left articular process and the spine. Most of the left ala is eroded away. The right ala lacks its cranial part and is eroded along its ventral border. For the average of three dimensions, KNM-BG 17822 is similar in size to female *Papio* first sacral vertebrae (Fig. 28C and D; Table 15, Size).

Description and functional features: The centrum is relatively narrow mediolaterally, compared both to its craniocaudal length and to its dorsoventral depth (Table 15, Indices 1 and 2), and does not consistently resemble any particular extant anthropoid in these features. The degree of mediolateral tapering between the cranial and caudal face is intermediate between the considerable tapering seen in cercopithecids and *Cebus* and the less tapered condition in extant hominoids and *Ateles* (Table 15, Index 3). The ventral border of the cranial face forms a moderately developed lip while the ventral surface of the centrum is relatively flat (Fig. 29E, a and b). The cranial half of the ventral foramina for the ventral rami of the first sacral nerves are present on each side of the caudal end of the centrum (Fig. 29H, c).

Cranially, the neural canal is relatively shallow dorsoventrally (Table 15, Indices 4

Table 14. Thoracic and lumbar vertebral indices and size comparisons.

	Index 1 Length/width ax100/b[1]	Index 2 Depth/length cx100/a	Index 3 Depth/width cx100/b	Index 4 Pedicle length dx100/a	Index 5 Pedicle proportions ex100/d	Size (a+b+c)/3
Pan troglodytes[2]	63.0[3]	120.7	75.9	71.4	49.6	24.4
Thoracic[4]	59-68	110-136	70-83	64-79	36-62	22.4-25.9
	3.1	8.9	4.1	5.0	10.1	
Lumbar[5]	57.9	133.2	76.9	70.7	52.9	
	51-66	117-148	68-85	60-84	39-68	
	4.1	10.1	6.1	9.8	11.4	
Hylobates spp.						
Thoracic	80.4	100.7	80.6	78.3	37.7	13.2
	72-89	91-117	73-87	74-85	29-54	10.7-15.1
	6.3	7.8	4.4	3.9	7.5	
Lumbar	80.4	97.8	77.0	69.5	39.9	
	69-95	85-111	67-82	64-81	25-52	
	8.3	9.2	4.6	5.2	10.9	
Papio cynocephalus	—	—	—	—	—	21.6
Male-Thoracic						20.0-23.5
Cercopithecus mitis						
Thoracic	87.9	70.7	61.9	88.0	27.9	11.9
	79-95	60-80	52-68	70-100	15-41	9.8-14.4
	5.2	6.6	4.7	9.2	8.8	
Lumbar	121.9	57.5	70.0	72.9	12.4	
	108-138	50-65	61-79	62-80	7-20	
	10.4	4.4	7.1	5.2	3.9	
Colobus polykomos						
Thoracic	87.0	82.7	71.8	79.2	37.1	16.7
	77-93	69-96	59-83	72-91	25-46	15.0-19.0
	6.1	9.4	8.1	5.1	7.7	
Lumbar	98.2	72.7	71.0	73.8	12.8	
	88-111	63-90	64-79	67-80	9-15	
	8.3	8.0	4.6	4.1	2.2	
Ateles spp.						
Thoracic	82.5	96.8	79.0	82.6	36.4	12.2
	72-98	78-113	66-88	70-93	24-50	10.4-15.0
	10.0	13.0	7.5	7.3	7.3	
Lumbar	76.0	102.3	76.9	77.9	39.1	
	59-91	91-116	68-85	69-91	26-48	
	10.7	9.3	5.7	7.7	6.8	
Cebus spp.						
Thoracic	91.6	83.0	75.3	86.2	37.5	10.4
	75-114	64-102	68-89	76-105	18-52	9.0-12.6
	10.4	10.5	6.9	8.7	11.5	
Lumbar	98.1	67.7	65.7	80.4	27.5	
	83-114	57-81	60-73	65-95	16-41	
	11.9	8.3	5.0	9.0	8.7	
Kenyapithecus sp.						
Thoracic, terminal						
KNM-BG 17826	84.1	90.5	76.1	71.7	35.8	22.3
Lumbar						
KNM-BG 15527	96.5	81.8	79.0	76.8	25.4	
Pliopithecus vindobonensis						
Thoracic, terminal						
Individual 1	96.3	74.4	71.7	80.9	30.4	16.1
Indet.	86.7	89.9	78.0	73.9	21.2	15.9
Thoracic, ?terminal						
KNM-WS 12603						
Proconsul heseloni	100.2	77.9	78.0	69.1	28.3	
Lumbar	90-110	77-79	71-85	64-73	27-30	
KNM-RU 2036CD, CY, & CZ, KNM-MV 5	8.2	0.9	5.5	4.3	1.3	
Proconsul nyanzae						
Thoracic, terminal						
KNM-MW 13142H	84.7	89.1	75.5	75.2	40.7	24.0
Lumbar						
KNM-MW 13142I, J, & K	96.8	86.1	83.2	71.6	19.5	
	92-100	83-90	83-84	69-74	17-21	
	4.5	3.6	0.5	2.3	2.1	
Indet	79.2	103.9	82.3	60.1	43.6	
Lumbar						
UMP 67.28						

[1] These are the measurements illustrated in Figure 28.
[2] $n=10$ for combined sex samples, $n=5$ for the single sex sample.
[3] Mean, range and S.D.
[4] Terminal thoracic
[5] Upper lumbars

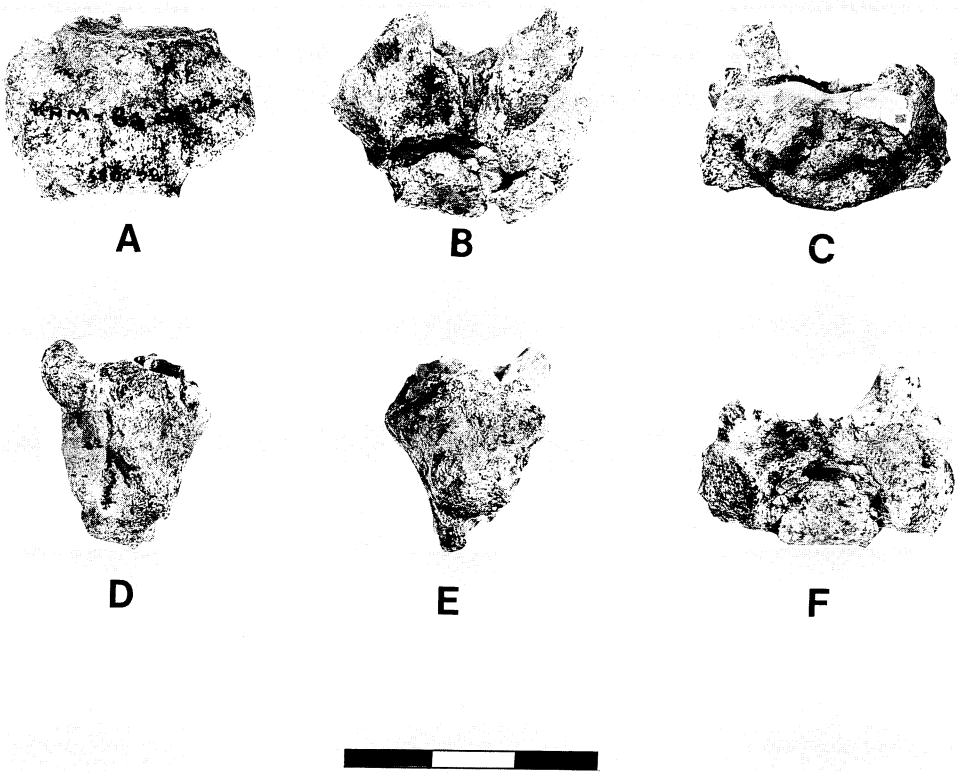

Figure 31. KNM-BG 17822 first sacral vertebra. A, ventral; B, dorsal; C, cranial; D, right; E, left; and F (caudal) views. Scale in cm.

and 5). Thus, in cranial view, the two laminae of the neural arch are oriented almost transversely, rather than sloping dorsally towards the midline (Fig. 29F, d). In dorsal view the cranial margins of the laminae slope caudally towards the midline, so that they make an open V-shape, as in non-hominoids, rather than the narrower U-shape characteristic of extant hominoids (Fig. 29G, e). The zygapophysis for the right lumbosacral joint is complete, although the articular surface is eroded ventrally (Fig. 29F and G, f). The preserved part of this surface is modestly curved in cranial view. It's angulation is greater than in most cercopithecids, less than in most extant hominoids, and close to the mean for *Cebus* (Table 15, Angle). The part of the zygapophysis that laterally buttresses the articular surface is more robust than is usual in extant anthropoids (Fig. 29G, g). Dorsally on the neural arch, the eroded base of the spine

Table 15. Sacral vertebral indices and size comparisons.

	Index 1 Width/length of centrum ax100/b[1]	Index 2 Depth/width of centrum cx100/d	Index 3 Width reduction dx100/a	Index 4 Depth/width of canal ex100/f	Index 5 Canal/ centrum depth ex100/c	Index 6 Centrum elevation gx100/b	Facet angle h	Size (a+b+d)/3
Pan troglodytes[2]	65.6[3]	66.9	77.4	48.3	33.0	33.7	71.0	30.1
	56-74	59-79	68-88	42-59	26-42	29-46	65-78	26.7-32.8
	6.1	5.6	6.9	5.0	5.4	5.9	5.0	
Hylobates spp.	71.8	60.3	65.1	50.8	35.1	16.6	67.3	14.9
	56-82	50-68	58-76	37-66	27-45	8-33	57-74	12.4-17.3
	9.2	5.0	6.0	9.7	5.6	9.0	5.2	
Papio cynocephalus	—	—	—	—	—	—	—	23.8
Male								23.1-24.7
Cercopithecus mitis	73.8	58.9	53.4	46.5	32.8	2.4	43.6	14.8
	61-88	54-63	46-61	37-63	26-41	1-4	34-55	12.4-17.4
	8.0	3.8	5.1	8.1	4.7	0.9	7.4	
Colobus polykomos	71.2	55.6	52.9	54.0	38.0	0.8	52.1	18.5
	64-75	53-60	47-68	45-63	34-49	0-1	40-62	16.1-21.0
	5.0	2.6	6.2	6.3	5.1	0.4	6.4	
Ateles spp.	73.0	65.1	75.4	56.9	50.9	22.1	74.2	16.1
	66-80	60-71	66-82	41-68	36-65	12-34	69-80	14.5-17.6
	3.5	3.2	5.4	8.2	10.4	6.2	4.0	
Cebus spp.	75.6	57.8	67.8	57.1	45.1	4.9	60.1	12.5
	67-91	52-65	61-73	37-81	31-63	1-8	53-65	11.6-14.8
	6.5	3.7	3.8	13.0	9.2	2.3	4.5	
Kenyapithecus sp. KNM-BG 17822	88.0	70.9	56.8	44.4	31.5	19.0	58	17.1
Pliopithecus vindobonensis Individual 1	87.4	63.3	51.1	39.9	26.5	7.7	56	17.5
Proconsul nyanzae KNM-MW 13142M	—	67.4	—	—	—	20.4	—	—

[1] These are the measurements illustrated in Figure 28.

[2] $n=10$ for combined sex samples, $n=5$ for the single sex sample.

[3] Mean, range and S.D.

is present in the midline (Fig. 29F and G, h). The caudal edge of the neural arch is eroded, so the dorsal foramina for the dorsal rami of the first sacral nerve are not present.

It is not possible to gain any idea of the overall morphology of the alae, due to erosion around most of the margins. However, on the right side, part of the articular surface for the sacroiliac joint (auricular surface) is preserved, together with the more dorsally placed area for attachment of the interosseous sacroiliac ligament. The auricular surface includes a dorsoventrally shallow cranial portion and a deeper caudal portion that extends as far as the dorsal surface of the bone, caudal to the interosseous ligament area, as found on extant non-hominoid sacra (Fig. 29E, i and j). The surface for the interosseous ligament is roughly concave. The cranial face of the centrum is somewhat elevated with respect to the adjacent roots of the alae, as in extant hominoids (Fig. 29H, k; Table 15, Index 6).

In most of its morphology, KNM-BG 17822 resembles extant non-hominoids, although in a general and non-specific way. In particular, the evidence of the articular area for the sacroiliac joint, although only partial, suggests that sacroiliac relationships in general are monkey-like, with the iliac blades oriented more towards the parasagittal plane than in extant hominoids (Ward, 1991, 1993). However, the cranial elevation of the centrum with respect to the alae, and the apparently quite small size of the surface for the lumbosacral joint are more extant hominoid-like. Ward (1991) suggests that an ape-like lumbosacral joint might reflect the absence of a tail. However, the totality of evidence from the axial skeleton strongly suggests its functioning in monkey-like, predominantly pronograde activities.

Comparisons with other catarrhine fossil sacral vertebrae: The *Kenyapithecus* sacrum resembles that of *Pliopithecus* (Zapfe 1960) in the mediolateral narrowness of the centrum (Table 15, Index 1), the shallowness of the neural canal (Table 15, Indices 4 and 5), and in the morphology of the auricular articular area. The *Kenyapithecus* specimen has a slightly deeper centrum and is slightly less tapered (Table 15, Indices 2 and 3). In comparable features, the sacra of *Kenyapithecus* and *Proconsul* (Ward, 1991, 1993) are quite similar. A robust articular process for the zygapophyseal articulation is shared by them to the exclusion all the taxa in the comparative samples. However, in *Proconsul* the auricular area is more linear, as in extant hominoids (Ward, 1991).

DISCUSSION AND CONCLUSIONS

Size and possible sexual size dimorphism: Where size comparisons can be made, all but one of the specimens described above fall into one of two size categories. KNM-BG 15071 (ulna), 17816, 17819, and 17820 (femora), 15535 (patella), and 17822 (sacral vertebra) are similar in size to the corresponding bones from female *Papio cynocephalus*. The other specimens are closer in size to those of male *Papio cynocephalus*. Assuming that the two groups do indeed come from male and female samples, and in terms of the known body weights of the *Papio* specimens used for the size comparisons, these data suggest body weights of approximately 22 kg for male *Kenyapithecus* and 11 kg for female *Kenyapithecus*. This in turn suggests a high

degree of sexual dimorphism in body size in *Kenyapithecus*, as was suggested above in light of the size difference between the two ulnar specimens. Among living anthropoids this degree of dimorphism is only found in *Papio*, *Nasalis*, *Pongo,* and *Gorilla* (Leutenegger and Kelley, 1977; Leutenegger and Cheverud, 1985). As stressed by Leutenegger and Kelley (1977) the factors underlying this degree of size dimorphism are complex and, as is evident from the above list, terrestriality is not a necessary correlate of extreme body size dimorphism. However, the data presented here raise at least the possibility of a degree of terrestriality in *Kenyapithecus*. The partial hallucial proximal phalanx, KNM- BG 17813 apparently comes from a larger individual than the other specimens. This suggests that the external hallux is disproportionately large in *Kenyapithecus*, or that it comes from a extraordinarily large male, or that it comes from a taxon not otherwise sampled from Nachola.

Positional behavior: Unfortunately many functionally informative anatomical regions and limb proportions, especially of the forelimb, are not available in the material described above. However, some indications as to function and possible positional activities can be gleaned from the material. The evidence of the vertebrae, particularly the lumbar vertebra, KNM-BG 15527 suggests that the trunk is long and narrow as in most pronograde, non-hominoid anthropoids. The tenuous evidence of the sacral vertebra, KNM-BG 17822, hints at the absence of an external tail. The limited evidence of the proximal ulnae, KNM-BG 15071 and 17824 suggests that the humeroulnar joint is not as stabilized as in extant hominoids, and may be capable of extending to about 180°. Also, there is evidence for powerful flexion and forearm rotation. These functions would be expected in activities, such as climbing, involving active reaching and hoisting. The morphology of the metacarpals, KNM-BG 15541 and 17807 suggests the importance of abduction-adduction in addition to flexion-extension at the metacarpophalangeal joints, and implies a versatility in hand placement and grasping during arboreal activities.

The evidence of the femoral specimens (particularly KNM-BG 17816 and 17819) and the patella, KNM-BG 15535 indicate that the working position of the hindlimb is in partial flexion and external rotation, with eccentric loading of the anterolaterally directed knee. This is similar to the hindlimb functioning of medium- and large-sized platyrrhines. The morphology of the distal fibula, KNM-BG 17810 is consistent with this interpretation. The orientation of the joint between the fibula and the lateral side of the talar trochlea is such that the talocrural joint can bear load effectively with the hindlimb in the partially flexed and externally rotated position.

The presence of an expanded medial process of the heel tuberosity of the calcaneus KNM-BG 17805 is particularly significant. Such a process is characteristic of arboreal taxa that use the intrinsic flexors independent of the extrinsic musculature, to produce adept grasping with the toes. This in turn reflects an ability to grasp branches of all orientations during arboreal activities, and implies a versatility of the locomotor repertoire. The first metatarsal KNM-BG 17814 and the phalanges consistently indicate that the joints of the fingers and toes are relatively broad. In addition, the middle phalanx 17808 and the terminal phalanges, KNM-BG 17748 and 17818 are also relatively short. These features indicate the unlikelihood of the presence of a suspensory capability, but are not otherwise contra-indicative of a secure arboreal grasping capability.

Thus, while the evidence is sparse, it suggests for *Kenyapithecus* a predominantly arboreal activity pattern in which quadrupedalism and vertical climbing using hoisting movements are important components of the locomotor repertoire. The degree of sexual dimorphism in body size and the presence of relatively short digits that are relatively wide distally may also indicate the presence of some terrestriality in addition to arboreality in the overall activity pattern. More definitive indicators of some terrestriality have been described for *Kenyapithecus africanus* from Maboko (McCrossin, 1994a, 1994b, McCrossin and Benefit 1994, 1995).

Comparisons with other Miocene Catarrhines: *Kenyapithecus* differs from *Pliopithecus* and small apes is having a more robust proximal ulna and proximal femur, in having a more mobile talocrural joint, and in having a relatively shorter hindfoot. It probably differs from *Dryopithecus* and *Sivapithecus* in the shape of the humeral trochlea, although this can only be deduced from the partial ulnar trochlear notch. Where comparisons can be made, the *Kenyapithecus* material is most similar to that of *Proconsul*. However, *Kenyapithecus* differs from *Proconsul* in several features that are important, both functionally and phylogenetically. Thus in *Kenyapithecus* the coronoid process is protuberant and the radial notch faces laterally, rather than anterolaterally. These are features shared with extant hominoids to the exclusion of *Proconsul*, and suggest that *Kenyapithecus* is more derived within hominoids than *Proconsul*. By contrast, the morphology of the sacroiliac joint is apparently more derived in *Proconsul* than in *Kenyapithecus*. Additionally, the *Kenyapithecus* calcaneus bears an enlarged medial process to the tuberosity. Apart from the sacral feature, these features indicate the greater importance of orthograde climbing in *Kenyapithecus*.

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